

EFFECT OF CLEAR-CUTTING ON THE DIVERSITY AND
DISTRIBUTION OF COLLEMBOLA IN WESTERN
NEWFOUNDLAND BALSAM FIR-
DRYOPTERIS AND EQUISETUM-RUBUS FORESTS

CENTRE FOR NEWFOUNDLAND STUDIES

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DAISY CHANDRIKA ARULNAYAGAM



**EFFECT OF CLEAR-CUTTING ON THE
DIVERSITY AND DISTRIBUTION OF COLLEMBOLA IN
WESTERN NEWFOUNDLAND BALSAM FIR- *DRYOPTERIS*
AND *EQUISETUM* - *RUBUS* FORESTS**

By
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ABSTRACT

The diversity and distribution of Collembola in western Newfoundland balsam fir forests were studied to determine if these forests return to their original conditions in respect to their biota, especially the collembolan community, when they regenerate after clear-cutting. The study was carried out in two different balsam fir forests of three different ages. They included balsam fir *Dryopteris* (FD) and balsam fir *Equisetum-Rubus* (FE) forest of 40 year old regrowth, 60 year old regrowth and old uncut forests. Within each type of forest two replicate sites of each of the three different ages were selected. Three types of samples, pitfall trap samples, microhabitat samples, and soil samples, were collected from the FD forest. Soil samples were collected from the FE forest.

Pitfall traps were used in the FD forest in summer 1992. Most of the species collected in pitfall traps were large, surface dwelling collembolans. Fifteen species were collected in the old forest and 14 and 19 species were collected in 40 and 60 year old forests, respectively. *Tomocerus flavescens*, *T. minor*, *Entomobrya multifasciata*, *Orchesella cincta* and *Neanura muscorum* were the dominant species in all sites. Pitfall traps did not reveal differences in collembolan communities between the different aged forests.

Various microhabitats were sampled in the FD forest in summer 1993, including rotten wood, tree holes, deciduous leaves, moss from live and dead tree, lichen from live and dead tree, and bark from live and dead tree. Thirty-five species of Collembola were collected from all microhabitats in the old forest. Twenty-seven and 32 species were collected in 40 year and

60 year old forests respectively. *Folsomia penicula* and *Isotomiella minor* were the dominant species in the microhabitats on the ground. One species, *Uzelia setifera*, was collected only in the microhabitats on trees.

Soil samples were collected in summers 1992, 1993 and June 1994 in the FD forest and in summer 1994 in the FE forest. Ten samples, each a cube of surface litter and soil, 10cm x 10cm x 10cm deep, were collected from each site on each sampling date. Each sample was cut into two horizontal halves, and each half was extracted separately in modified Berlese funnel. A total of 53 species representing 29 genera of Collembola were collected from the soil samples. The mean densities and diversity of the Collembola collected in the upper halves of the soil samples were higher than those of the lower halves on each sampling date, except *Tullbergia granulata* was more abundant in the lower halves. Mean densities of Collembola in the FD forest varied between 174.4 to 849.2/1000cm³ and in the FE forest 209.0 to 572.0/1000cm³. Seasonal patterns were observed in the proportion of Collembola occurring in the lower half of the samples and in the total number of Collembola collected in the FD forest. In the late summer the proportion of Collembola in the lower half of the samples was higher than that of the early summer, and the total abundance was higher in June and August than in July.

In both FD and FE forests, old sites had the highest species diversity and abundance. In the FD forest, the 40 year old site had the lowest species diversity and the 60 year old forest had the lowest density. In the FE forest, 40 year old sites had both lowest species

diversity and density. Two species, *Folsomia penicula* and *Isotomiella minor* were the dominant species in both forest types, comprising about 50-70% of the total number of Collembola. *Tomocerus flavescens*, *Stenogastrura hiemalis* and *Isotoma (Desoria) beta* were collected only in the old forest. *T. minor* and *Willowsia huski* were restricted to the regrowth forests. *Isotomurus palustroides*, *Neeus minutus* and *Neeus incertus* were collected only in the FE forest.

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This study indicates that clear-cutting does have a long term effect on the abundance and diversity of Collembola. Forty year old forests had the least diversity, and species diversity increased with forest age. Old forests contained three Collembola species that were not collected from regrowth forests.

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1. INTRODUCTION

1.1 Historical Review

The rate of movement of essential nutrients by decomposition is an important regulator of forest productivity (Anderson *et al.* 1981). Soil animals play a major role in decomposition and nutrient cycling through the fragmentation of dead organic matter, which enhances leaching of soluble materials and increases the surface area available for microbial colonization. They graze on microbes on organic substrates and thus stimulate microbial activity, influence microbial community structure, and release nutrients immobilized by the microflora. Soil animals are also a reservoir of nutrients which become available to plants when they die (Seastedt and Tate 1981) and they contribute to soil fertility by depositing faeces and improving soil porosity (Berg and Pawluk 1984).

Clear-cutting, a forest management practice that has been recognized as creating many rapid and long-lasting changes (Chandler and Peck 1992), is a common operational forestry practice in North America. Although clear-cut forest harvesting increases the yield of fibre per unit area, its long-term effect on site productivity is unknown. Since soil animals are intimately involved in decomposition and nutrient cycling, a better understanding of the influence of clear-cutting of forest on soil animals may provide insight into the effect of this practice on long-term site productivity.

There have been few studies on the effect of clear-cutting on soil animals, especially soil microarthropods in North America. Most studies on the effects of forest harvesting on

soil microarthropods have been conducted in Europe. Huhta *et al* (1967, 1969) and Huhta (1976) studied the impact of clear-cutting on microarthropods densities. They reported temporary increases in densities of most microarthropod taxa followed by declines over the following seven years. Huhta (1976) attributed this response to increased amounts of food resources, represented by organic matter in soil after clear-cutting, followed by subsequent declines in organic matter in clear-cut areas. A similar study was carried out on soil microarthropods in a tropical rain forest in Nigeria (Lasebikan 1975). The overall results suggested that clearing reduced both the number of species and the number of individuals of certain soil faunal groups in the short term.

There have been only three North American studies published on the effects of clear-cutting on microarthropod populations. Vlug and Borden (1973) studied soil Acari and Collembola populations affected by logging and slash burning in a coastal British Columbia coniferous forest. They reported that the abundance of Collembola fell to half the original value soon after clear-cutting, with the faunal composition and proportion of species unchanged. Seastedt and Crossley (1981) attributed a decrease in microarthropod populations in the forest floor following cable logging and clear-cutting in the southern Appalachian of North Carolina to higher temperatures ($>40^{\circ}\text{C}$). However, they reported that Collembola densities showed no change.

Bird and Chatarpaul (1986) studied the effect of whole-tree and conventional forest harvest on soil microarthropods in Ontario, Canada. Their results showed that Collembola

exhibited a slight increase in abundance on the cut forest in comparison with the uncut forest. They also reported that the density of Collembola in the mineral layer (0-5 cm) was not affected by clear-cutting. All of the North American studies were carried out soon after harvesting or clear-cutting (1-4 years) of the forest sites. No studies on the long term effect of forest harvesting on soil microarthropods have been conducted in North America.

1.2 Importance of Collembola in Forest Soils

Collembola are among the most abundant of soil arthropods and play an important role in soil formation through litter decomposition and nutrient recycling especially in forest soils (Takeda 1973). They are globally distributed, occurring even in the Antarctic, and colonize a variety of biotopes where they often occur in high population densities (Eisenbeis and Wichard 1987). Over 6000 collembolan species in about 500 genera have been described world-wide (Greenslade 1991) of which at least 520 species are estimated to occur in Canada (Marshall *et al.* 1990).

The taxonomy of the Holarctic Collembolan species is fairly well known (Christiansen & Bellinger 1980). Collembolan communities of various forest soils have been studied (Usher 1970, Nijima 1971, Persson *et al.* 1980, Peterson & Luxton 1982, Bird and Chaptarpaul 1986, Huhta *et al.* 1986, Marshall *et al.* 1990) and the ecology of various species described (Poole 1961, MacLean *et al.* 1977, Vegter *et al.* 1988).

Collembola were chosen for this study because they are the commonest soil insects.

Because of their large numbers and high diversity in the soil, they could possibly be used as indicators of soil conditions (Marshall 1967). For example, collembolan populations do respond to habitat changes such as changes in humidity of soil surfaces and changes in soil temperature (Mitra *et al* 1977, Kaczmarek 1975, Teuben and Smidt 1992). They also can be used as indicators of soil fertility as they are usually found in high numbers where their main foods, fungi and decaying material, are abundantly available.

1.3 Biology of Collembola

Collembola can be divided into two ecological groups, those which live on or near the surface and those which live in the soil. These are called epedaphic (suborder Symphypleona and families Poduridae, Entomobryidae and Isotomidae) and euedaphic (families Onychiuridae and Hypogasuridae) life forms respectively (Eisenbeis and Wichard 1987).

Surface dwelling species possess well developed springing organs, eyes, and elongate antennae. Some breathe by means of tracheae; the majority through the skin. No Collembola are more than a few millimetres in length but those normally inhabiting the deeper layers tend to be even smaller than surface dwelling species, a characteristic associated with the size of the soil pore spaces in which they live and move about. Euedaphic forms have no tracheae and have reduced springing organs, a permeable body covering, short antennae, and simple ocelli. All collembolans possess a ventral tube on abdominal segment 1, which can be everted or retracted and can be used to attach the animal to the substratum (Christiansen 1964).

In collembolans that lack a tracheal system, the ventral tube and the general body surface are used for gaseous exchange. The discontinuous wax layer of the cuticle and the hydrofuge hairs confer some degree of protection against desiccation as well as against flooding, for the hairs trap a film of air and this permits cuticular respiration to continue even under submerged conditions. The evolution of a tracheal system in the more advanced species allows for a greater waterproofing system and therefore permits a degree of independence from moist soil making possible the colonization of more exposed habitats without the danger of desiccation or suffocation (Brown 1978).

Collembola show varying degrees of tolerance to different environmental factors such as soil structure and type, the presence of micro-flora and moisture. Indeed, the presence or absence of a species could be an indication of micro-habitat conditions. So far as soil micro-flora are concerned, it is fairly certain that some species live in the gut of collembolans as symbionts, probably assisting in the digestion of plant material (Brown 1978). The distribution of fungi upon which most Collembola feed, must also be a controlling factor in their distribution. Fungi and collembolan populations may also compete for available moisture (Brown 1978).

Since collembolans are unable to burrow they must perforce use soil pores in order to move through soils. These spaces are generally smaller in regions where decomposition is taking place and where food is more abundant (Brown 1978). Also, where greater amounts of vegetable matter is present, the soil is less prone to dry out. Vertical distribution is

therefore governed by several factors - the size of the species and pore space, moisture content, and available food (Brown 1978).

The ability to move vertically in surface layers of the soil is of advantage to the smaller species which, although usually associated with deeper levels within the soil, may nevertheless range through the soil profile. These vertical migrations mean that the animals can move upwards when the upper soil layers are moist in spring and autumn and avoid drought and extremes of temperature by moving downwards in summer and winter. In this way they can take advantage of optimal conditions of temperature and moisture (Christiansen 1964).

The mouthparts of collembolans vary from one group to another. Broadly speaking those which chew their food (a wide variety of genera such as *Folsomia*, *Onychiurus*, and *Hypogastrura*) possess well-developed mandibles and a molar plate capable of rasping hard plant material. Biting forms (most of the sminterids) have strong, toothed mandibles but no molar plate while in sucking forms (most Neanuridae, Brachystomellidae, Odontellidae) the mandibles are reduced to stylets for piercing and sucking juices (Christiansen 1964). Some specialist carnivorous species (genus *Friesea*) feed on rotifers, proturans, and tardigrades whereas phytophagous forms may select one species of plant as their food. *Isotoma grandiceps* feeds upon other collembolans (Christiansen 1964). Although a correlation of mouthparts with the type of food selected would make a tidy classification of types, in point of fact many species consume a wide variety of organic food according to what is available (Brown 1978).

Among the predators of Collembola, mites are clearly of greatest importance. Second in importance to mites are pseudoscorpions, staphylinid and carabid beetles, and young or small centipedes. In addition to these, quite a wide variety of animals feed upon Collembola either under special conditions or in unusual habitats. These include spiders, fish, frogs, predacious Hemiptera, ants, and snails (Christiansen 1964). The majority of parasites of Collembola are gregarines and nematodes. Eggs appear susceptible to fungus attack, and fungi may cause severe damage to juvenile forms (Christiansen 1964).

Most Collembola are univoltine developing from egg to adult within one year. Some are bi- or multivoltine, producing two or more generations within that time. Sperm is usually transferred indirectly from male to female by the male depositing either a spermatophore or a free droplet on the substratum which is later taken up by the female. Development and hatching of the eggs depends on the species and on the temperature of the soil. Instar 1 larvae upon hatching from eggs are six-legged and resemble adults in all but size, pigmentation and sexual maturity. Thereafter, the young moult several times giving rise to successively larger, more darkly coloured individuals until the adult instar which is deemed to be that at which maximum size and sexual maturity is attained. Adults may continue to moult. The number of larval instars varies according to species (Christiansen 1964). The production of large numbers of juveniles gives rise to population peaks at certain times of the year. These peaks are influenced by local environmental factors, particularly temperature. Declines in population, alternating with peaks, have been observed to occur mainly in January and July in northern latitudes and have been attributed largely to predation by mesostigmatid mites

(Brown 1978).

1.4 Research Objectives

Harvesting and clearing of commercial forests have made an impact on the earth's environment including effects on structures of plant and animal communities, long term impacts on ecological processes and biological resources and especially changes in local and regional biodiversity. Because of the biodiversity crisis in forest environments, fears have been expressed that a large portion of earth's species could be lost within a short period of time (Wilson and Peter 1988). The rates and nature of recent human impacts on these environments have raised concerns about the long term health and integrity of these systems (Bonan and Shugart 1989). To evaluate and to take necessary steps to solve this problem, Forestry Canada has started a program to undertake studies on commercially important forest types. Their aim is to compare the degree of community changes among sites with different histories (eg harvesting and disturbances). The current study is included within this program to compare the collembolan communities of an old forest with no history of disturbance to those forests growing under similar environmental conditions but with known histories of disturbances in western Newfoundland. The emphasis was placed on comparing old forest with regrowth forest that was approaching harvestable size again in order to determine if the collembolan fauna of regrowth fauna returns to pre harvested conditions before the next harvesting cycle begins.

There is very little information available on the collembolan fauna of Newfoundland.

The only previous study was that of Stach (1966) who reported on the Collembola species collected by Polish zoologists Prof. S. Feliksiak and Prof. T. Jaczewski during their zoogeographical studies on Newfoundland and Nova Scotia, in 1938. He identified 7 genera and 7 species of Collembola in Newfoundland, all of which were new to this island. There has been no study done on the impact of forest harvesting on soil microarthropods in Newfoundland forests.

The objectives of this study are to:

1. characterize the collembolan communities from different types of commercial forests of western Newfoundland
2. determine long-term effects of forest harvesting on Collembola community structure.

2 MATERIAL AND METHODS

2.1 Study Sites

The study sites were located in western Newfoundland south of Corner Brook at elevations of approximately 75 to 450 metres in the Long Range Mountains. The sites included three different aged stands of two balsam fir forest types: a moist, fertility rich balsam fir - *Dryopteris* (FD) forest and a wet, moderately rich balsam fir - *Equisetum* - *Rubus* (FE) forest (Meedes and Moores 1989). Two replicate sites of each forest type and of each, three different ages were selected. Explanation of terminology is follows: forest - forest type i.e. FD or FE; Area - portion of a forest of a given age within which sampling sites were located; Site - specific location from which samples were collected.

The study sites are designated as followed. Locations of study sites, and abbreviations for forest types, ages and sites are as follows. Study site locations are also indicated on a map (Fig 1.).

A. Control - Old growth forest, never cut. Maximum tree age 80+ years

1. Balsam fir - *Dryopteris* forest (FDO)

- a. Site 1. 2 km East Martin Pond near Little Grand Lake (FDO-1)
- b. Site 2. Bakeapple Brook near Little Grand Lake (FDO-2)

2. Balsam fir - *Equisetum* forest (FEO)

- a. Site 7. 2 km East Martin Pond near Little Grand Lake (FEO-7)
- b. Site 8. Bakeapple Brook near Little Grand Lake (FEO-8)

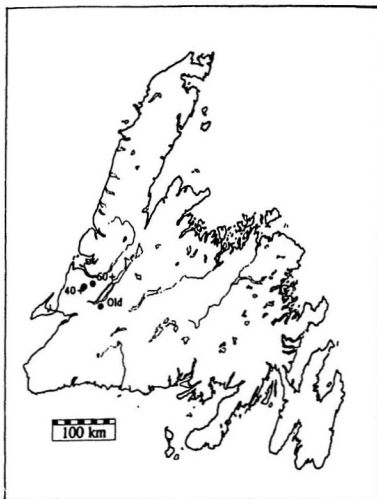


Figure 1. Map of Newfoundland indicating locations of the three different sampling areas of western Newfoundland balsam fir forests (Age of forest in each area: old - 80+ year old uncut; 40+ - 40+ year old regrowth; 60+ - 60+ year old regrowth. Two fir - *Dryopteris* (FD) and two fir - *Equisetum* (FE) sites located in each area).

B. 40-year-old forest

1. Balsam fir - *Dryopteris* forest (FD40)
 - a. Site 3. Cooks Pond near Stag Lake (uphill from access road) (FD40-3)
 - b. Site 4. Cooks Pond near Stag Lake (downhill from access road) (FD40-4)
2. Balsam fir - *Equisetum* forest (FE40)
 - a. Site 9. Cooks Pond near Stag Lake (downhill from access road) (FE40-9)
 - b. Site 10. Cooks Pond near Stag Lake (downhill from access road) (FE40-10)

C. 60-year-old forest

1. Balsam fir - *Dryopteris* forest (FD60)
 - a. Site 5. Near Loggers school road on Trans Canada Highway (TCH) 10 km south from Corner Brook (uphill from TCH) (FD60-5)
 - b. Site 6. Near Loggers school road on TCH 10 km south from Corner Brook (downhill from TCH) (FD60-6)
2. Balsam fir - *Equisetum* forest (FE60)
 - a. Site 11. Near Loggers school road on TCH 10 km south from Corner Brook (downhill from TCH) (FE60-11)
 - b. Site 12. Near Loggers school road on TCH 10 km south from Corner Brook (downhill from TCH) (FE60-12)

2.2 Habitat characteristics

2.2.1 Climate

The study area has a temperate, maritime-boreal climate of cool summer and mild winter. The average surface soil temperature in July is 18.5°C and in January is 0.2°C. Precipitation is evenly distributed over the year with an average total of 364 mm from January to April and 394 mm from May to September. The ground is generally snow covered from December to May (Banfield 1983).

2.2.2 Vegetation and Soil

Both FD and FE forests have been characterized by Meades and Moors (1989) as one in which balsam fir, the principal softwood species, grows in association with black (*Picea mariana*) and white (*Picea glauca*) spruce, and yellow birch (*Betula lutea*) and mountain maple (*Acer spicatum*) occur as minor species. In FD forest, *Dryopteris spinulosa*, a fern, is the dominant understorey species (75-90% cover). The FE forest is characterized by *Equisetum* (horse tails) and *Rubus*, which occur rarely in the FD forest. Habitat descriptions of FD and FE forests and site descriptions of FD forest are given in Tables 1 & 2 respectively. Photographs of distribution of trees and understorey vegetation of FD and FE forest habitats are given in Figures 2-5. Data on principal vegetation types and densities of trees (number/m²) were provided by Dr. Ian Thompson, Forestry Canada. These data were collected using a 2 metre² quadrat within which the percentage of the soil surface covered by the principal vegetation types was estimated. The data of characteristics of the mineral soil were also provided by Forestry Canada. Two samples from each site were collected in spring 1993 for the soil analysis.

2.3 Sampling Methods

Three types of samples were collected from each FD forest, namely pit-fall trap samples, microhabitat samples and soil samples. Pit-fall traps collected epedaphic species from the soil surface and microhabitat samples collected species from specific habitat types. The soil samples provided a quantitative estimate of collembolan populations within the soil (euedaphic forms). The pit-fall trap samples were collected only in summer 1992 and

Table 1. Characteristics of fir - *Dryopteris* (FD) and fir - *Equisetum* (FE) forests in western Newfoundland balsam fir forests (after Meedes and Mores 1989)

Site characteristics	Forest type	
	<i>fir - Dryopteris</i>	<i>fir - Equisetum</i>
Slope	mid to upper slopes	lower concave slopes
Moisture	somewhat moist	somewhat wet to wet
Soil Type	silt loam to sandy loam; Orthic podzol soil; seepage 40 cm; organic horizon 10-20 cm; rooting 50 cm	loam to sandy loam; gleyed regosol soil; muck surface; shallow rooting
pH	5.0 - 5.5	4.5 - 4.7
Fertility	rich to very rich	medium to rich
Principal shrub and understorey vegetation	<i>Dryopteris spinulosa</i> (75-95%) <i>Acer spicatum</i> <i>Viburnum edule</i> <i>Sambucus pubens</i> <i>Rubus idaeus</i> <i>Ribes glandulosum</i> <i>Rhytidiadelphus loreus</i> <i>Hylocomium umbratum</i> <i>Streptopus roseus</i> <i>Solidago macrophylla</i>	<i>Carex leptoneura</i> <i>Dryopteris phegopteris</i> <i>Equisetum sylvaticum</i> <i>Thuidium recognitum</i> <i>Mnium punctatum</i> <i>Athyrium filix-femina</i> <i>Circaea alpina</i> <i>Aster puniceus</i> <i>Geum rivale</i> <i>Sphagnum squarrosum</i> <i>Rhytidiadelphus squarrosus</i> <i>Rubus pubescens</i> <i>Galium triflorum</i> <i>Cinna latifolia</i> <i>Cornus stolonifera</i> <i>Rhytidiadelphus triquetrus</i> <i>Viola incognita</i> <i>Mitella nuda</i> <i>Rubus triste</i> <i>Ribes lacustre</i> <i>Dryopteris disjuncta</i>

Table 2. Site descriptions of the three different aged FD forests from western Newfoundland. Details of soil, vegetation and tree density are given in Tables 3-5.

	Sites		
	FDO	FD40	FD60
Age in Years	old (80+)	40+	60+
Latitude, Longitude	48°38'N 57°47'W	48°52'N 58°05'W	48°52'N 57°56'W
Elevation	400 - 450 m	75 - 100 m	300 - 350 m
Moisture	somewhat moist	slightly less moist than old	more moist than other two areas
Ground Cover	moss layer in small patches, a few small shrub, lots of fern	moderate moss cover with lots of fern, litter and lichen	little moss cover, heavy shrubs and overgrown vegetation
Tree Density	tall mature trees, well spaced, fair amount of shading, lots of oldman's beard and dead wood	big, well branched trees, fairly close together, less shading and little dead wood	same as FD40, less amount of shading, little dead wood



Figure 2. Photograph showing the trees and understorey of a balsam fir- *Dryopteris* (FD) forest - site FDO-2.



Figure 3. Photograph showing the understorey vegetation of a FD forest -site FDO-1.



Figure 4. Photograph showing the trees and understorey of a balsam fir- *Equisetum* (FE) forest - site FEO-8.



Figure 5. Photograph showing the understorey vegetation of a FE forest - site FEO-8.

microhabitat samples were collected only in summer 1993. Only soil samples were collected from FE forest.

2.3.1 Pit-fall Trap Samples

Megan Davis kindly allowed insects she collected in pitfall traps during her study of forest Coleoptera to be analysed for the presence of large, active, surface dwelling Collembola. A trap was made up of two different sized plastic pots, a small pot 11.5 cm diameter and 6.8 cm deep and a larger flower pot 12.8 cm diameter and 10.5 cm deep. The small pot, placed inside the larger, contained propylene glycol and collected animals falling into the trap whereas the larger pot supported the small pot in the ground and allowed the small pot to be removed for emptying without disturbing the trap setting. Traps were set out by digging a hole in the ground in which the larger flower pot was set with the rim flush with the soil surface. The small pot was placed tightly inside the large pot so that animals fell into it. A wire handle fixed to the small pot allowed it to be removed easily from the flower pot. A 20 cm x 20 cm wooden plate supported above the trap on legs made of nails formed a rain-cap to prevent flooding.

In each site twenty pit-fall traps were placed 3 m apart parallel to the line from which soil samples were collected. Traps were emptied four times over the summer. Animals were sieved from the collecting agent and transferred into alcohol bottles in the field. They were then taken to the lab, sorted under a dissecting microscope, and stored in 70% ethanol for identification and counting. Collembola species were ranked in terms of the relative

abundance of specimens collected in the traps. These rankings were abundant (more than 10 specimens); common (5-10 specimens) and rare (1-5 specimens).

2.3.2 Microhabitat Samples

Various microhabitats were sampled in 1993, once in July and once in August. The nine microhabitats were rotten wood, tree holes, deciduous leaves, moss from live trees, moss from dead trees, lichen from live trees, lichen from dead trees, bark from live trees and bark from dead trees. A paper bag (16 cm x 7.5 cm x 30 cm) full of material from each type of microhabitat was collected from each site. Samples were taken to the lab and extracted in Berlese funnels. The insects from the tree bark and lichens were collected by a floatation method. First the samples were broken into small pieces and transferred to a large bowl with 70% ethanol. Then by stirring the liquid gently the insects were separated from the samples and floated to the surface. The floating insects were then sieved from the suspension and transferred into bottles of alcohol.

2.3.3 Soil Samples

Each soil sample was a cube of surface litter and soil 10 cm x 10 cm x 10 cm deep. This was collected by placing a wooden template (10 cm x 10 cm) on the ground and cutting the soil along each side of the template to a depth of 10 cm using a knife. The soil cube was then carefully removed was cut in half horizontally. Each half sample was stored in a paper bag, placed in a cooler and taken to the field station for immediate extraction. Ten samples were collected from each site on each sampling period (20 samples were collected in July 1992).

They were taken 3 m apart along a straight line perpendicular to the access road and starting far enough into the forest to avoid any edge effects of the road. Sampling was done twice in 1992 (15 & 23 July and 29 August), three times in 1993 (1 & 7 June, 6 & 13 July and 17 & 27 August) and once (June 22 & 23) in 1994 in the FD forest, and twice (5 & 6 July and 22 August 1994) in the FE forest.

Modified Berlese funnels housed in an unheated building, in which temperature averaged about 15-20°C, were used to extract the animals. The samples were extracted in a 20°C closed room in 1992. The limited ventilation in that room increased the temperature and humidity inside the room and may have affected the extraction efficiency. In 1993 and 1994, samples were extracted in a large room with open windows where the room temperature followed the outside temperature which seldom exceeded 20°C throughout the extraction.

Each Berlese funnel contained a sieve made from 15 cm inside diameter PVC piping cut into 5 cm high rings with 2 mm mesh nylon screen glued to the bottom of a ring. A double layer of cheese cloth was placed over the mesh to reduce the amount of debris falling through the screen. The sieve was placed inside the lip of a plastic funnel (17.5 cm diameter and 20 cm long). Each sieve was separated by about 2.5 mm from the edge of the funnel for ventilation with 3 screws placed around its lower edge. A 60 ml plastic bottle containing 70% ethanol was attached to the bottom of the funnel to collect organisms (Figs. 6 and 7). The top of the collection bottle had several holes drilled in it to produce air circulation inside the



Figure 6. Photograph of a set of Berlese funnels, top view, used to extract Collembola from soil and microhabitat samples.



Figure 7. Photograph of a set of Berlese funnels, lateral aspect, used to extract Collembola from soil and microhabitat samples.

funnel in order to reduce condensation.

A group of Berlese funnels was made by placing 9 funnels together (each in a 15 cm diameter hole) on a bristle board plate supported by a 70 cm x 55 cm rectangular wooden frame. This frame was fixed on and supported by 50 cm high wooden poles. A 7.5 W light bulb was used as a light source above each funnel. Bulbs were connected in parallel and fixed on a 70 cm x 40 cm rectangular wooden frame which was fixed to the wooden poles and adjusted to position lights 15 cm above the funnels. Altogether 120 funnels were used. Each sample was extracted over a period of 7 days. Animals leaving the sample were collected and stored in 70% ethanol. Collembola and other animals were picked out later and stored in glass vials until identified and counted.

2.4 Identification

Collembola were cleared by leaving them in lactic acid for 5 - 7 days and then complete specimens were temporarily mounted in glycerine on depression slides. Identification was done using a compound microscope. All collembolans were identified to species level or as far as possible. Identifications of representative specimens of all taxa were confirmed by Dr. Jan Addison (Forest Pest Management Institute, Sault Ste. Marie, Ontario). Taxonomic names were according to the following authors: Maynard 1951, Scott 1951, Christianson and Bellinger 1980, Christianson 1990.

2.5 Statistical analysis

The species list was examined to determine the taxonomic composition and the dominant species at each site. Both qualitative and quantitative data files were used for the statistical analysis. Total numbers of specimens/sample/sampling date were used for the diversity indices and ANOVA and total numbers of specimens/species/year were used for rarefaction curves. Taxa means/sampling date were used for Principal Component Analysis (PCA), Discriminant Function Analysis (DFA), Two Way Indicator Species Analysis and Cluster analysis. Qualitative data were used to compare sites through similarity indices and cluster analysis.

Shannon-Weiner diversity indices and evenness values were calculated by using DIVERS program of Krebs (1991). The rarefaction curves for the expected number of species in a sample of a given number of Collembola were calculated by using the RAREFACT program of Krebs (1991) but modified by Ms. R. Thompson to accommodate sample sizes up to 10,000 individuals. One-way and two-way ANOVA was used to test for the significance of spatial and seasonal differences ($\alpha = 0.05$) by using MINITAB (Ryan *et al* 1976).

PCA was used to compare the three different aged forests in both FD and FE habitats on the basis of their collembolan fauna. The relationship between the Collembola diversity and the ecological characteristics (vegetation and soil) of the FD habitat was also analysed using PCA. Mean values of all measured ecological (soil and vegetation) characteristics and

abundance of Collembola species for each site were included in the PCA. Discriminant Function Analysis was used to identify characteristics differing between the 3 different ages of forests in both habitats. Both the PCA and Discriminant Function Analysis were performed in SPSS.

Cluster analysis, an agglonative classification method, was carried out to identify associations of species within the study area. The mean abundance of Collembola species for each sampling date (for quantitative analysis) and the presence-absence data (for the qualitative analysis) were used, and the analyses were run using procedure CLASSIFY in SPSS. Euclidean distance was used to measure association between sites and sites were clustered using group average clustering. Two Way Indicator Species Analysis, a divisive classification technique, was carried out to identify patterns within the species distribution data and to identify the indicator species for groups defined by this classification. Three pseudospecies cut levels (20, 60, & 100) were used to define the crude scale of the species abundance and the program TWINSpan (Hill 1979; Carlton 1985) was used to run this analysis. Pseudospecies refer to different abundance levels of a species and are treated as separate entities in the analysis.

3. RESULTS

3.1 Habitat Characteristics

3.1.1 Soil Characteristics

Thirteen soil variables were measured in FD forest sites in 1993, including particle size, quantities of selected organic and inorganic substances and pH of the soil (Table 3). Organic matter and carbon, ash, sodium, phosphorus and pH were in low quantities whereas the other 6 inorganic substances were relatively abundant in all 3 ages of forests. FDO and FD60 areas had relatively high concentrations of calcium and phosphorus in their soil whereas FDO and FD40 areas had high amounts of nitrogen in their soil. High amounts of aluminium, and iron were found in regrowth sites. The amounts of carbon, potassium, organic matter, and magnesium were higher in FDO than in FD40 and FD60 areas. The other six variables did not show much difference between different ages of forests.

Results of PCA analysis of the FD forest on the basis of soil characteristics are presented in Table 4 and Fig 8. The first factor extracted from this analysis accounted for 62.9% of the variation, whereas the second factor explained 19% of the variation. Potassium, magnesium, nitrogen, phosphorus, organic matter and carbon had high positive loadings and iron, aluminium and ash had high negative loadings on the first factor, whereas calcium and sodium had high positive loadings and particles < 2 mm had high negative loading on Factor 2. pH had low values on both factors. FD60-6 and FD40-3 were separated from other sites on the basis of factor 1 and the other 4 sites were clustered together (Fig 8).

Table 3. Mean soil characteristics of L, F and H layers of FD forest study sites (2 samples/site were analysed; data provided by Forestry Canada).

Soil characteristics	Forest Age		
	FDO	FD40	FD60
Aluminium (ppm)	587.7	1657.6	1377.9
Ash (ppm)	14.2	44.9	26.1
Calcium (ppm)	1370.8	664.9	1774.2
Iron (ppm)	938.7	4018.8	2256.4
Potassium (ppm)	781.1	578.3	642.1
Magnesium (ppm)	553.1	526.5	461.7
Nitrogen (ppm)	111.9	102.5	54.4
Sodium (ppm)	97.5	51.0	288.3
Phosphorus (ppm)	78.1	44.2	68.1
Carbon (%)	45.6	30.0	40.2
Organic Matter (%)	80.7	51.8	69.3
pH	3.8	4.1	3.8
Particles < 2 mm	9.5	15.9	10.0

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Table 4. Loadings of the soil characteristics on the first two factors extracted by Principal Components Analysis of FD study sites.

Soil Characteristics	Factor 1	Factor 2
Potassium	.98631	.08659
Iron	-.96019	-.21525
Aluminium	-.91460	-.30677
Magnesium	.87111	-.15205
Nitrogen	.85759	-.19635
Phosphorus	.85158	-.06938
Ash	-.82319	-.52966
Organic matter	.82221	.52823
Carbon	.80959	.56415
Calcium	.31235	.92494
Sodium	-.33812	.86426
Particles < 2 mm	-.52513	-.70386
pH	-.03865	.11135
% Variance explained	62.9%	19.0%

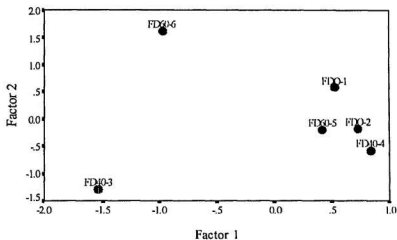


Figure 8. Principal Component ordination of the six FD sites based on soil characters. Soil characteristics and factor loading scores are presented in Table 6.

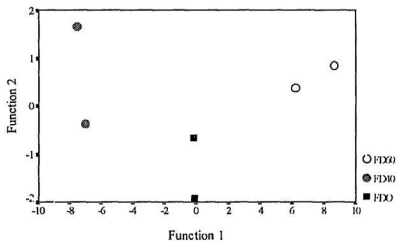


Figure 9. Discriminant Function ordination of the FD sites based on soil characters. Soil characters and function correlations are given in Table 7.

The Discriminant Function Analysis for the soil variables separated the sites of the three ages of forest with one hundred percent success (Fig 9, Table 5). Function 1 had four variables with significant correlation (sodium, pH and calcium positively and particles < 2 mm negatively) and Function 2 had nine variables with significant correlations (iron, aluminium and ash negatively and rest of the variables positively) (Table 6).

3.1.2 Vegetation Characteristics

Twenty four vegetation characteristics of the FD forest were analysed. These characteristics included the percentage of the ground covered or shaded by various types of plants or debris (16 variables, Table 7), and plant diversity and mean densities of shrubs and trees (8 variables, Table 8). Most of these characteristics did not significantly differ among areas. Deciduous litter (38%) was abundant in area FD60 whereas sphagnum (5.5%), feather moss (49.7), low fern (30%) and logs (7.4%) were more abundant in area FDO. Fern litter in area FD40, and low and medium shrubs in area FDO were low respectively compared to the other two areas. Conifer litter, tall fern and low shrubs were more abundant in FD40 and FD60 than in the FDO area.

PCA of the 24 vegetation characteristics resulted in the extraction of the first two principal component factors which accounted for 38.4% and 26.8% of variation (Table 9). Five characteristics had high positive loadings on Factor 1, namely Foliage height diversity low, small tree density, shrub density, deciduous litter and tall fern. Four variables, feathermoss, sphagnum, log diameter and logs had high negative loadings. Poor separation

Table 5. Classification results of the Discriminant Function Analysis for the soil characteristics of the FD study sites.

Actual Group	No. of Cases	Predicted Group Membership		
		1	2	3
Group 1 (FDO)	2	2 100.0%	0 .0%	0 .0%
Group 2 (FD40)	2	0 .0%	2 100.0%	0 .0%
Group 3 (FD60)	2	0 .0%	0 .0%	2 100.0%

Percent of "grouped" cases correctly classified: 100.00%

Table 6. Summary table of the soil characteristics showing highest significant correlation on Discriminant Functions 1 and 2 in FD study sites.

Soil characteristics	Function 1	Function 2
Sodium	.99081*	.12682
pH	.68675*	-.15863
Calcium	.62364*	-.41228
Particles < 2mm	-.48769*	.33441
Magnesium	.00003	-.97225*
Nitrogen	.01819	-.87181*
Phosphorus	-.54726	-.83696*
Ash	-.09127	.80835*
Organic matter	.09355	-.80521*
Potassium	-.27059	-.80078*
Iron	.23477	.79437*
Aluminium	-.02824	.75562*
Carbon	.08934	-.71581*

* denotes largest absolute correlation between each variable and any discriminant function.

Table 7. Mean values of vegetation characteristics (n=50) of the FD study sites, expressed as percentage of soil covered (several characters may overlap so that the total percent cover exceeds 100%. Data provided by Dr Ian Thompson, Forestry Canada).

Vegetation characteristics	Forest Age		
	FDO	FD40	FD60
Deciduous litter	12.7	17.5	38.0
Fern litter	4.8	0.2	3.8
Conifer litter	11.0	17.2	18.2
Slash	8.6	6.9	9.6
Sphagnum	5.5	0.3	0.6
Feather moss	49.7	28.6	29.0
Lichen	0.1	0.1	0.1
Lycopodium	0.1	0.0	0.0
Gram	0.1	0.1	0.0
Forbs	20.1	23.7	18.4
Low shrub	5.0	18.6	28.1
Medium shrub	0.6	1.9	3.2
Low fern	21.5	18.6	28.1
Tall fern	6.4	11.4	10.9
Logs	7.4	4.8	2.5

Table 8. Mean tree density (number/m²) and diversity (Brillouin's diversity index) of FD study sites (data provided by Dr. Ian Thompson, Forestry Canada).

Vegetation characteristics	Forest Age		
	FDO	FD40	FD60
Foliage height diversity (FDH)			
Low	0.8	1.2	1.4
Medium	1.2	0.8	1.2
Top	1.2	0.1	1.1
Shrub density	0.10	0.16	0.37
Shrub diversity	2.63	2.30	3.32
Small tree density	0.04	0.12	0.18
Tree density	0.11	0.27	0.15
Dead tree density	0.12	0.17	0.14

Table 9. Loadings of the vegetation characteristics on the first two factors extracted by Principal Components Analysis of FD study sites.

Vegetation Characteristics	Factor 1	Factor 2
FDH low	.98434	-.15661
Small tree density	.94987	.03803
Feathermoss	-.91573	.38939
Shrub density	.87884	.07892
Log diameter	-.86191	-.02282
Logs	-.85492	-.31749
Deciduous litter	.77926	-.11237
Sphagnum	-.76203	.22726
Tallfern	.72549	-.44709
Dead small tree	.14378	-.96266
FDH medium	-.21561	.91406
Low fern	.30410	.91047
Slash	.04617	.89123
Fern litter	-.31718	.82817
Medium shrub	.22807	.04031
Low shrub	.00282	.36230
Coniferous litter	-.03258	.24048
FDH top	.13711	-.46141
Tree density	.30465	-.25809
Shrub diversity	.29979	-.26310
Forb	.24373	-.37225
Lycopodium	-.33866	.59540
Gram	-.22568	.40478
% variance explained	38.4%	26.8%

of different ages of forests was obtained in this analysis and the sites within forests of each age were more or less equally separated from each other (Fig 10).

Function 1 of the Discriminant Function Analysis separated FDO areas from FD40 and FD60 areas, but sites of the latter two were clustered together (Fig 11). Approximately 83% classification was achieved for the 3 areas of FD forest habitat (Table 10). The vegetation characteristics showing highest correlation on Discriminant Functions 1 and 2 are given in Table 11. Twelve variables had high correlations on Discriminant Function 1, with the highest correlation being for log diameter, logs, and sphagnum (negatively) and forbs, and low shrubs (positively).

3.2 Collembola Fauna

A total of 61 species representing 29 genera and six families of Collembola was collected in aggregate from all types of samples and both forest habitats (Table 12). Forty-six taxa were identified to species and one taxon could be identified only to family. Among these, 27 genera and 53 species occurred in the soil quadrat samples; thirteen genera and 22 species of Collembola were collected in pitfall traps (Table 13); and 22 genera and 38 species were recovered from microhabitat samples (Table 14-16).

3.3 Pitfall Trap Samples

Most of the Collembola collected in the pitfall traps were epedaphic forms, and the abundance of the species were low in pitfall traps compared to soil and microhabitat samples.

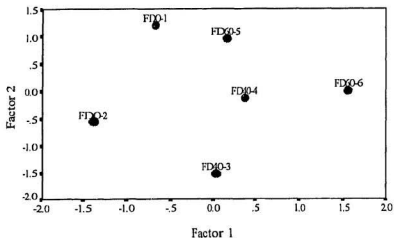


Figure 10. Principal Component ordination of the six FD sites based on vegetation characters. Vegetation characteristics and factor loadings are presented in Table 9.

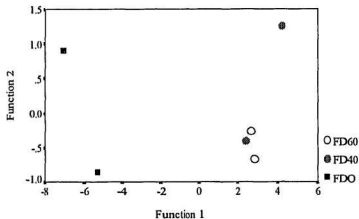


Figure 11. Discriminant function ordination of the FD sites based on vegetation characters. Vegetation characteristics and function correlations are given in Table 10.

Table 10. Classification results of the Discriminant Function Analysis for the vegetation characteristics of the FD study sites.

Actual Group	No. of Cases	Predicted Group Membership		
		1	2	3
Group 1 (FDO)	2	2 100.0%	0 .0%	0 .0%
Group 2 (FD40)	2	0 .0%	1 50.0%	1 50.0%
Group 3 (FD60)	2	0 .0%	0 .0%	2 100.0%

Percent of "grouped" cases correctly classified: 83.3%

Table 6. Summary table of the vegetation characteristics showing highest significant correlation on Discriminant Functions 1 and 2 in FD study sites.

Vegetation characteristics	Function 1	Function 2
Log diameter	-.87801*	.40143
Forbs	.82431*	-.15013
Logs	-.70709*	.70401
Low shrub	.68497*	.33051
Shagnum	-.53304*	.12363
Medium shrub	.52804*	.48600
Fern litter	.45545*	-.37010
Shrub density	.41303*	-.16916
FHID top	-.34857*	.23284
Tall fern	-.34157*	-.09892
Feather moss	-.27379*	.11388
Conifer litter	.07487*	.02221
Gram	.35899	-.91685*
Dead small tree	.08357	.88359*
Low fern	-.03370	-.78515*
Shrub diversity	.35417	.72911*
Lycopodium	.35417	.72911*
Lichen	-.34799	-.71196*
Tree density	-.42595	-.70296*
Small tree density	-.40534	-.53652*
Slash	.48845	-.52932*
FDH medium	.09043	-.45264*
FDH low	.14422	-.30654*
Deciduous litter	-.09469	-.09825*

* denotes largest absolute correlation between each variable and any discriminant function.

Table 12. Species list of Collembola collected from FD and FE forest habitats, summer 1992 to 1994 (species order follows Christiansen and Bellinger 1980).

ORDER - COLLEMBOLA

SUBORDER - ARTHROPLEONA

DIVISION - Poduromorpha

FAMILY - Hypogastridae

Hypogastrura (Mitchellania) loricata Yosii
Hypogastrura (Hypogastrura) humi (Folsom)
Stenogastrura hiemalis Christiansen
Willemia denisi Mills
Willemia intermedia Mills
Friesea sublimis Macnamara
Friesea alaskella Fjellberg
Pseudachorutes (Pseudachorutes) subcrassoides Mills
Pseudachorutes (Pseudachorutes) aureofaciatus (Harvey)
Anurida (Micranurida) pygmaea (Börner)
Anurida (Micranurida) furcifera (Mills)
Neanura (Neanura) muscorum (Templeton)

FAMILY - Onychiuridae

Onychiurus (Protaphorura) similis Folsom
Onychiurus (Onychiurus) paro Christiansen
Onychiurus (Archaphorura) affinis Ågren
Tullbergia (Tullbergia) granulata Mills

DIVISION - Entomobryomorpha

FAMILY - Isotomidae

Uzelia setifera Absolon
Anurophorus (Pseudoanurophorus) binoculata (Kseneman)
Folsomia penicula Bagnall
Meisotoma grandiceps (Reuter)
Micrisotoma achromata Bellinger
Isotomiella minor (Schäffer)
Isotomurus (Isotomurus) sp
Isotomurus pulustroides Folsom
Isotoma (Desoria) ekmani Fjellberg
Isotoma (Desoria) notabilis Schäffer
Isotoma (Desoria) trispinata MacGillivray
Isotoma (Desoria) manitobae Fjellberg
Isotoma (Desoria) hiemalis Schott
Isotoma (Desoria) sp 1
Isotoma (Desoria) sp 2
Isotoma (Desoria) sp 3
Isotoma (Desoria) sp 4

Table 12 Cont....

Isotoma (Desoria) sp 5
Isotoma (Desoria) sp 6
Isotoma (Desoria) sp 7
Isotoma (Desoria) sp 8
Isotoma (Isotoma) viridis Bourlet
Isotoma (Vetagopus) beta Christiansen

FAMILY - Entomobryidae

Orchesella cincta (Linnaeus)
Entomobrya (Entomobrya) multifasciata (Tullberg)
Entomobrya (Entomobrya) nivalis (Linnaeus)
Entomobrya (Entomobrya) comparata Folsom
Willowsia buski (Lubbock)
Lepitocyrtus cyaneus Tullberg
Tomocerus (Pogonognathellus) flavescens Tullberg
Tomocerus (Tomocerus) minor (Lubbock)
Tomocerus (Tomocerus) sp

SUBORDER - SYMPHYPLEONA

FAMILY - Neelidae

Neelus (Megalothorax) minimus (Folsom)
Neelus (Neelides) minutus (Folsom)
Neelus (Megalothorax) incertus (Börner)

FAMILY - Sminthuridae

Sminthurides (Sminthurides) lepus Mills
Arrhopalites hirtus Christiansen
Arrhopalites benitus (Folsom)
Arrhopalites diversus Mills
Sminthurinus (Sminthurinus) quadrimaculatus (Ryder)
Sminthurinus (Sminthurinus) henshawi (Folsom)
Sminthurus sp 1
Sminthurus sp 2
Dicyrtoma fusca (Lubbock)
Dicyrtoma (Ptenothrix) sp 1
Dicyrtoma (Ptenothrix) sp 2
Dicyrtoma (Ptenothrix) sp 3

Table 13. Collembola taxa collected in pitfall traps from the FD forest, summer 1992 (rank - more than 10 specimens ***-abundant, 5-10 specimens **-common, 1-5 specimens *-rare)

SPECIES	SITES		
	FDO	FD40	FD60
<i>Hypogastrura loricata</i>	***	**	**
<i>Hyogastrura humi</i>	**		**
<i>Pseudoscorpionus aureofaciatus</i>	*	**	**
<i>Neanura muscorum</i>	*	***	***
<i>Metisotoma grandiceps</i>	**	*	*
<i>Isotomurus</i> sp	***		*
<i>Isotoma viridis</i>	***	**	*
<i>Isotoma</i> sp 6	*	*	
<i>Isotoma</i> sp 7	*		*
<i>Isotoma</i> sp 8	*	*	*
<i>Orchesella cincta</i>		***	***
<i>Entomobrya nivalis</i>	**		
<i>Entomobrya multifasciata</i>	***	***	**
<i>Entomobrya comparata</i>	*	*	**
<i>Willowsia buski</i>			**
<i>Lepidocyrtus cyaneus</i>			*
<i>Tomocerus flavescens</i>	***		
<i>Tomocerus minor</i>		***	***
<i>Sminthurinus quadrimaculatus</i>			*
<i>Dicyrtoma (Ptenothrix)</i> sp 1	**	***	*
<i>Dicyrtoma (Ptenothrix)</i> sp 2		**	**
<i>Dicyrtoma (Ptenothrix)</i> sp 3		*	**

Table 14. Collembola taxa collected in microhabitat samples from the FDO forest, summer 1993 (microhabitats: A-rotten wood, B-tree hole, C-deciduous leaves, D-moss from live tree, E-moss from dead tree, F-lichen from live tree, G-lichen from dead tree, H-bark from live tree, I-bark from dead tree. Rank ***-abundant, **-common, *-rare)

SPECIES	MICROHABITATS								
	A	B	C	D	E	F	G	H	I
<i>Hypogastrura loricata</i>		*	***	***		*	*		
<i>Hypogastrura humi</i>	*	**	***	***	**				
<i>Willenia dentisi</i>	*	*	*	*	*	**			
<i>Willenia intermedia</i>			*	*					
<i>Friesea submitis</i>	*	**	*	*					
<i>Pseudochorutes subersoides</i>	*		***		*				
<i>Pseudochorutes aureofaciatus</i>		*	*	*	*				
<i>Neamura muscorum</i>	*	*	*	*					
<i>Onychiurus similis</i>	**	**	***	*	*				
<i>Onychiurus paro</i>	**	**	*	*	*	*			
<i>Onychiurus affinis</i>	**	*	**	**					
<i>Tullbergia granulata</i>			*						
<i>Uzelia setifera</i>					*	***	**	***	**
<i>Folsomia penicula</i>	***	***	***	**	***				
<i>Metisotoma grandiceps</i>		**	**	*	*				
<i>Isotomella minor</i>	**	***	***	*	**				
<i>Isotomurus</i> sp	*		**	***	***	*	*		
<i>Isotoma notabilis</i>	**	**	*	**	*				
<i>Isotoma trispinula</i>	*	*							
<i>Isotoma viridis</i>		*	*	*	**	***	*		
<i>Isotoma manitobae</i>	*	*	*	**					
<i>Isotoma hiemalis</i>	*	*		*	*				
<i>Isotoma</i> sp 2	**	*	*						
<i>Isotoma</i> sp 3	**	*	*						
<i>Isotoma</i> sp 4	*		*						
<i>Entomobrya multifasciata</i>	*	*		**	***		*	***	
<i>Tomocerus flavescens</i>		*	*	**	*	*		*	
<i>Sminthurides lepus</i>	*	*	**		*				
<i>Arrhopalites benitus</i>	*	**	*		*				
<i>Arrhopalites hirtus</i>	*	*							
<i>Arrhopalites diversus</i>			*						
<i>Sminthurinus quadrimaculatus</i>			*	*	*				
<i>Sminthurinus henschawi</i>			*						
<i>Sminthurus</i> sp 1	*	*							
<i>Sminthurus</i> sp 2		*			**				

Table 15. Collembola taxa collected in microhabitat samples from the FD40 forest, summer 1993
 (microhabitats: A-rotten wood, B-tree hole, C-deciduous leaves, D-moss from live tree, E-moss from dead tree, F-lichen from live tree, G- lichen from dead tree, H-bark from live tree, I-bark from dead tree. Rank ***-abundant, **-common, *-rare)

SPECIES	MICROHABITATS								
	A	B	C	D	E	F	G	H	I
<i>Hypogastrura loricata</i>			**	***		**			
<i>Hypogastrura humi</i>		*	*		*				
<i>Willemia intermedia</i>	*		*	*					
<i>Friesia submilis</i>	*	**	*	*	*				
<i>Pseudolachnites aureofasciatus</i>			*	*					
<i>Neanura muscorum</i>		*	*	*	*				
<i>Onychiurus similis</i>	**	***	***	*	*				
<i>Onychiurus para</i>	*	*	**	*					
<i>Onychiurus affinis</i>	**	*	**						
<i>Tullbergia granulata</i>						*			
<i>Uzelia setifera</i>					*	*	**	**	
<i>Folsomia penicula</i>	**	***	***	***	**				
<i>Metisotoma grandiceps</i>		*	*	**					
<i>Isotomiella minor</i>	**	**	***	*	**				
<i>Isotomurus</i> sp	**		*	***					
<i>Isotoma notabilis</i>		*	*	*					
<i>Isotoma trispinata</i>	*	**	**		*				
<i>Isotoma</i> sp 3				*	*	*			
<i>Isotoma</i> sp 4		*			*				
<i>Entomobrya multifasciata</i>	**	*	***	*	**	**	*		
<i>Tomocerus</i> sp		*	*	**					
<i>Sminthurides lepus</i>	*		*	*	*				
<i>Arrhopalites benitus</i>			*		*				
<i>Arrhopalites hirtus</i>		*			*				
<i>Arrhopalites diversus</i>	*								
<i>Sminthurinus henschawi</i>		*		*					
<i>Dicyrtoma fusca</i>		*	*	*	*				

Table 16. Collembola taxa collected in microhabitat samples from FD60 forest, summer 1993 (microhabitats: A-rotten wood, B-tree hole, C-deciduous leaves, D-moss from live tree, E-moss from dead tree, F-lichen from live tree, G-lichen from dead tree, H-bark from live tree, I-bark from dead tree. Rank ***-abundant, **-common, *-rare)

SPECIES	MICROHABITATS								
	A	B	C	D	E	F	G	H	I
<i>Hypogastrura loricata</i>			*		**	**			
<i>Hypogastrura humi</i>	*		*		*				
<i>Willemia intermedia</i>	*	*	*	**	**				
<i>Friesea submilis</i>	**	**	*	**					
<i>Pseudachorutus aureofaciatus</i>		*		*	**				
<i>Neanura muscorum</i>	*	**	**	**					
<i>Onychiuroides similis</i>	**	**	***	*	***				
<i>Onychiuroides paro</i>	**	**	**	*					
<i>Onychiuroides affinis</i>	***	**	***	*	*				
<i>Tullbergia granulata</i>		*	**	*					
<i>Uzelia setifera</i>					**	**	**	***	*
<i>Folsomia penicula</i>	***	***	**	***	***				
<i>Metisotoma grandiceps</i>		*			*				
<i>Isotomiella minor</i>	**	**	***	**	***				
<i>Isotomurus</i> sp	**	**		*	*				
<i>Isotoma notabilis</i>		**	*	*	*	*			
<i>Isotoma trispinata</i>	*		**	*	*				
<i>Isotoma viridis</i>		*			**	**		*	
<i>Isotoma hiemalis</i>	*			**					
<i>Isotoma</i> sp 3	*	*							
<i>Orchesella cincta</i>	***	***	***	**	***				
<i>Entomobrya multifasciata</i>	*		*	**	*	*	*	*	
<i>Tomocerus</i> sp		*	**	*	*	*			
<i>Neelus minimus</i>		**							
<i>Sminthurides lepus</i>			*						
<i>Arrhopalites benitus</i>	*								
<i>Arrhopalites diversus</i>			*						
<i>Arrhopalites hirtus</i>	**								
<i>Sminthurinus quadrimaculatus</i>		*							
<i>Sminthurinus henshawi</i>	*								
<i>Dicyrtoma fusca</i>	**	*		**					
<i>Sminthurus</i> sp 1			**						

Fifteen species of Collembola in FDO area, 14 species in the FD 40 area, and 19 species in FD60 area were collected in the pitfall trap samples (Table 13). *Hypogastrura loricata*, *Neanura muscorum*, *Pseudachorutus aureofasciatus*, *Entomobrya multifasciata*, and *Ptenothrix* sp 1 were collected in all 6 sites. *Entomobrya multifasciata* was the most numerous species and together with *Tomocerus flavescens* in FDO area and *Tomocerus minor* in FD40 and FD60 areas, comprised approximately 90% of specimens at each site. *Tomocerus flavescens* was collected only in the FDO area and *Willowsia buski*, *Lepidocyrtus cyanens* and *Sminthurinus quadrimaculatus* were collected only in the FD60 area. *Tomocerus minor*, *Orchesella cincta*, and *Ptenothrix* sp 3 and 4 were trapped from FD40 and FD60 areas. *Isotomurus* sp, *Metisotoma grandiceps* and *Isotoma viridis*, which were common in the FDO area, were collected rarely in the regrowth forests and *Neanura muscorum*, a rare species in the FDO area, was common in FD40 and FD60 areas.

3.4 Microhabitat Samples

Thirty eight species of Collembola were collected from the microhabitat samples, distributed as follows: FDO area - 35 species; FD40 area - 27 species; and FD60 area - 32 species (Tables 14-16). Species composition and density differed between microhabitats. Highest species abundance and diversity were found in deciduous leaves followed by tree hole, rotten wood and moss samples. Six species of Collembola were collected from lichen and bark from live and dead trees. *Uzelia setifera* was found only in microhabitat samples from trees. *Isotomurus* sp, *Tomocerus flavescens*, *T. minor*, *Tomocerus* sp, and *Entomobrya multifasciata* were also found in samples collected from trees at all sites. *Folsomia penicula*

and *Isotomiella minor*, the two dominant species in soil samples, were the dominant species in all microhabitats found on the ground. The remaining species were present also in the soil samples.

3.5 Soil samples

3.5.1 FD Sites

3.5.1.1 Vertical distribution of Collembola

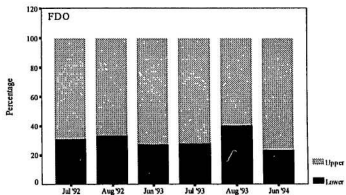
The mean densities of the Collembola collected in the upper halves of the soil samples were higher than those of the lower halves on each sampling date (two-way ANOVA, $p = 0.000$, $df=1$). This also applied to all species except *Tullbergia granulata* which was more abundant in the lower halves of the sample. About 60-75 % of the total number of Collembola were collected from the upper samples (Fig 12). The number of species collected was also higher in the upper halves (Appendix B). Seasonal variation was observed in the percentage of total Collembola occurring in each half sample over time in the FD forest. In both FDO and FD40 areas, samples collected in August (especially August 1993) had relatively more Collembola in the lower layers than those of June and July.

3.5.1.2 Total Numbers of Collembola

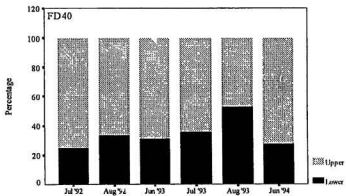
Within the FD forest, old forest generally had the highest densities of Collembola (Fig 13) followed by FD40 forest. FD60 forest had the lowest Collembola density. Mean densities in the FD forest varied between 338.8 - 849.2/1000cm³ (in FDO) and 277.6 - 607.2/1000cm³ (in FD40) and 174.4 - 363.4/1000cm³ (in FD60) (Appendix A). The total mean density of

Figure 12. Percentage of the total number of Collembola collected in the upper and lower halves of soil samples in the FD forest, summer 1992 to 1994 (A- FDO; B - FD40; C- FD60).

A



B



C

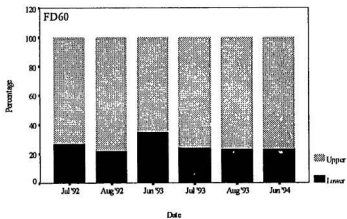
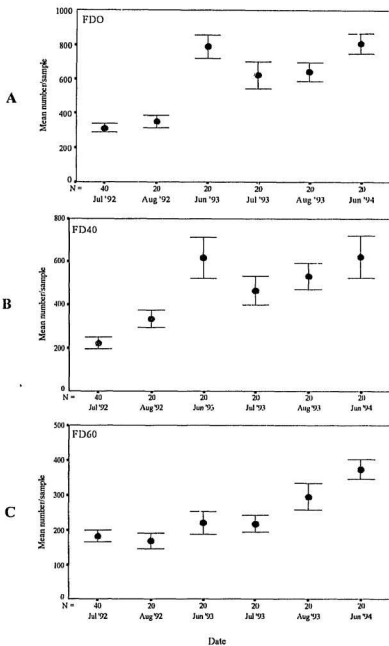


Figure 13. Mean and standard error of the number of specimens of Collembola per sample collected in the FD forest, summer 1992 to 1994 (A - FDO; B- FD40; C- FD60).



Collembola collected in 1992 was less than that of 1993 and 1994 in all ages of forest. Densities in the FDO and FD40 areas were similar in 1993 and 1994 whereas densities in the FD60 area increased from June and July 1993 to June 1994. Total numbers tended to be lower in July than in June or August (Fig 13).

3.5.1.3 Faunal Composition

Members of the family Isotomidae made up approximately 75% of the total number of Collembola in soil samples. *Folsomia penicula*, a common species in much of North America (Christiansen & Bellinger 1980), was the most abundant species in all areas on all 6 sampling periods, comprising 35-70% of the total number of Collembola. The next most abundant taxa, in decreasing order of abundance were *Isotomiella minor*, *Isotoma notabilis*, *Onychiurus paro*, *O. affinis*, and *Tullbergia granulata* (Figs 14-16). The remaining 48 species each contributed less than 1% of the total number of individuals.

The abundance of *Folsomia penicula* was higher in 1993 and 1994 than in 1992 collections. *Isotomiella minor* and *Isotoma notabilis* were collected in high numbers in 1994. The relative abundances of the other three most abundant species as well as the uncommon species were similar in all three year's samples (Figs 14-16). *Friesea alaskella* and one unidentified species of the family Hypogastruridae were collected only in 1994 in the FD forest (Appendix A).

Although most of the species were common to the different ages of FD forest, some

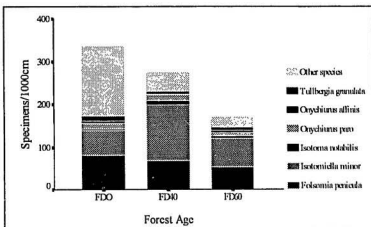


Figure 14. Bar graphs of mean densities of the five most abundant species and the remaining Collembola species collected from the FD forest, summer 1992.

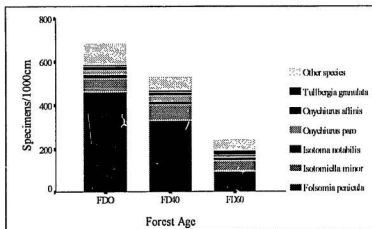


Figure 15. Bar graphs of mean densities of the five most abundant species and the remaining Collembola species collected from the FD forest, summer 1993.

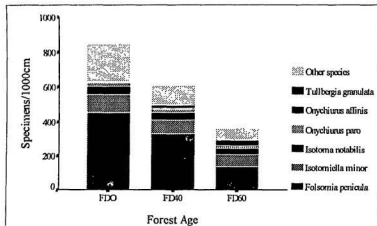


Figure 16. Bar graphs of mean densities of the five most abundant species and the remaining Collembola species collected from the FD forest, summer 1994.

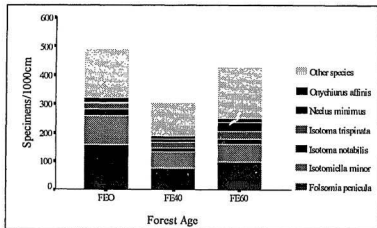


Figure 17. Bar graphs of mean densities of the five most abundant species and the remaining Collembola species collected from the FE forest, summer 1994.

differences were found in species composition. *Stenogastrura hiemalis* and *Tomocerus flavescens* were collected only in the FDO area (Appendix A) whereas *Tomocerus minor*, *Orchesella cincta*, *Willowsia buski* and *Dicyrtoma fusca* were restricted to FD40 and FD60 areas (Appendix A).

3.5.1.4 Diversity Indices and Evenness

Collembola species diversity, as indicated by Shannon-Weiner diversity indices and evenness values, varied between different age of forests and overtime (Figs 18 and 19). On most sampling dates the upper halves of the samples had higher species diversity and evenness values except August 1992, where the lower halves had higher species diversity than the upper ones. The FD60 area showed the highest diversity index values in both layers of the samples on all sampling dates except July 1992 where the FDO area had the highest values.

The highest diversity index (3.5) and evenness values (0.72) in the FD forest were obtained in sites FDO-1, July 1992 and in FD60-5, August 1992 respectively. The lowest value of diversity (1.6) was obtained in site FD40-4, July 1993 and the lowest evenness values (0.32) was obtained in site FDO-1, July 1993 (Appendix B).

3.5.1.5 Rarefaction

Rarefaction curves derived from the total number of species and individuals of Collembola collected in each of the six sites of the FD forest in 1992, 1993 and 1994 are given in Figures 20-22. Although the total number of specimens collected from each site

Figure 18. Shannon-Weiner diversity indices for Collembola in the upper half of soil samples collected from the three different aged FD forest, 1992 to 1994.

Figure 19. Shannon-Weiner diversity indices for Collembola in the lower half of soil samples collected from the three different aged FD forest, 1992 to 1994.

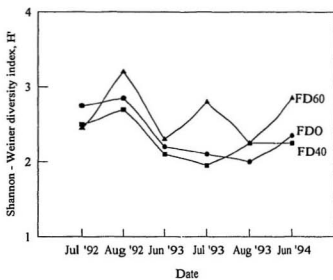
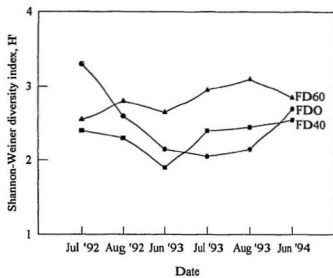


Figure 20. Rarefaction curves for expected number of Collembola species in samples of various size collected from FD forests, summer 1992.

Figure 21. Rarefaction curves for expected number of Collembola species in samples of various size collected from FD forest, summer 1993.

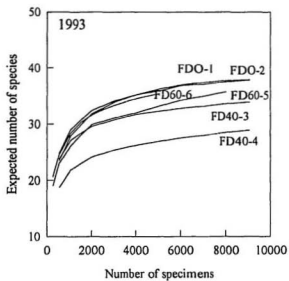
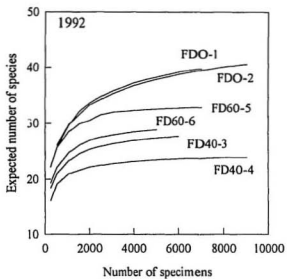
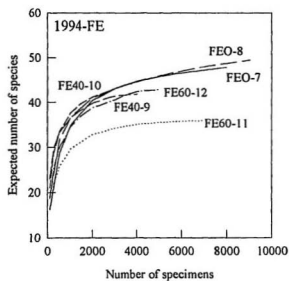
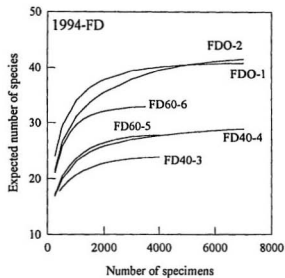


Figure 22. Rarefaction curves for expected number of Collembola species in samples of various size collected from FD forests in June 1994.

Figure 23. Rarefaction curves for expected number of Collembola species in samples of various size collected from FE forest, summer 1994.



varied from 1992 to 1994, the expected numbers of species per given number of specimens collected were always highest in the old growth site. FD60 had the second highest and FD40 had the least number of expected species per given number of specimens.

3.5.1.6 Principal Components Analysis (PCA)

The overall results of PCA of Collembola mean abundance in each over all sampling dates (n=6) in FD forest separated the FDO sites from the FD40 and FD60 sites (Fig 24). Sites FDO-2 and FDO-1 were separated from the other sites on the basis of factor 1 and FD60-6 was separated from the other sites on the basis of factor 2. Twenty five Collembola species had high loadings on factor 1, which accounted for 45.8% of the overall variation among the distribution of Collembola species (Table 17). Except for *Tullbergia granulata*, the rest of these species had positive loadings on Factor 1. Factor 2 explained 24.7% of the variation. Eight species of Collembola had high loadings on factor 2 of which only one, *Isotoma manitobae* had negative loadings.

3.1.4.4 Discriminant Functions Analysis

Discriminant analysis using the Collembola data separated samples from the 3 different aged FD forests with 100% correct classification (Fig 25 and Table 18). The first 10 Collembola species showing the highest correlations on Discriminant Functions 1 and 2 are given in Table 19. FDO was separated from FD40 and FD60 forests on the basis of this function. Although the distributions of 19 Collembola species were associated with function 1, none was statistically significant. The highest values were for *Onychiurus paro* and

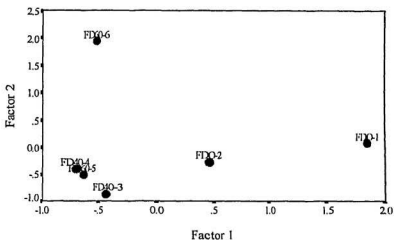


Figure 24. Principal Component ordination of the six FD sites based on the mean abundance of Collembola over all sampling dates ($n=6$). Collembola species and function loadings are given in Table 17.

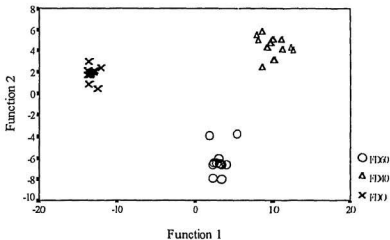


Figure 25. Discriminant function ordination of FD forest sites based on the mean abundance of Collembola in each site on each date. Each point represents mean sample values on a given sampling date. Collembola species and function correlations are given in Table 19.

Table 17. Loadings of Collembola species on the first 2 factors extracted by Principal Component Analysis of FD study sites

Collembola species	Factor 1	Factor 2
<i>Isotoma ekmani</i>	.99532	-.01421
<i>Arrhopalites benitus</i>	.98760	-.04387
<i>Tomocerus minor</i>	.98291	.00406
<i>Isotomiella minor</i>	.98188	-.02669
<i>Metisotoma grandiceps</i>	.97708	-.17178
<i>Isotoma</i> sp 2	.95695	.23084
<i>Stenogastrura hiemalis</i>	.93408	-.06298
<i>Isotoma hiemalis</i>	.92155	-.09611
<i>Isotoma</i> sp 3	.92117	.01414
<i>Sminthurus</i> sp 1	.91838	.10836
<i>Hypogastrura humi</i>	.91501	-.09538
<i>Isotoma</i> sp 4	.90878	-.06595
Unidentified sp.	.90516	.04148
<i>Isotoma</i> sp 5	.88943	.29624
<i>Sminthurides lepus</i>	.86341	-.25748
<i>Arrhopalites hirtus</i>	.85727	-.30009
<i>Tomocerus</i> sp	.82871	-.06863
<i>Isotomurus</i> sp	.81506	-.10785
<i>Sminthurinus quadrimaculatus</i>	.75975	.52743
<i>Arrhopalites diversus</i>	.74923	-.14762
<i>Pseudochorutus subcrassoides</i>	.74570	-.21271
<i>Tomocerus flavescens</i>	.73415	.05078
<i>Tullbergia granulata</i>	-.72483	.34456
<i>Sminthurinus henshawi</i>	.71675	.17400
<i>Folsomia penicula</i>	.61682	-.41345
<i>Lepidocyrtus cyaneus</i>	-.25516	.95126
<i>Isotomurus palustroides</i>	.27365	.94173
<i>Willowsia buski</i>	-.30982	.92759
<i>Friesia alaskella</i>	.29505	.90461
<i>Isotoma manitobae</i>	-.41448	.81351
<i>Entomobrya multifasciata</i>	-.55045	.78912
<i>Sminthurus</i> sp 2	.59836	.74189
<i>Neanura muscorum</i>	-.40073	.72483
% Variance explained	45.8%	24.7%

Table 18. Classification results of the Discriminant Function Analysis from the FD forest.

Actual Group	No. of Cases	Predicted Group Membership		
		1	2	3
Group 1 (FDO)	12	12 100.0%	0 .0%	0 .0%
Group 2 (FD40)	12	0 .0%	12 100.0%	0 .0%
Group 3 (FD60)	12	0 .0%	0 .0%	12 100.0%

Percent of "grouped" cases correctly classified: 100.00%

Table 19. Summary table of Collembola species showing highest on Discriminant Functions 1 and 2 of FD study sites (significant value for 95% confidence level is 0.32 when n=36).

Species	Function 1	Function 2
<i>Onychiurus paro</i>	.18902*	.16587
<i>Tullbergia granulata</i>	.16917*	-.00834
<i>Sminthurinus henschawi</i>	.14790*	.10309
<i>Isotoma hiemalis</i>	-.10172*	.07192
<i>Onychiurus similis</i>	-.09413*	.04531
<i>Friesia allaskella</i>	-.07549*	-.01740
<i>Isotoma sp 4</i>	-.07536*	.02026
<i>Tomocerus flavascens</i>	-.07116*	-.00908
<i>Isotomurus sp</i>	-.06552*	.02915
<i>Arrhopalites diversus</i>	-.06515*	.05603
<i>Willowsia buski</i>	.06937	-.40004*
<i>Neanura muscorum</i>	.03913	-.37402*
<i>Tomocerus minor</i>	.00186	.33456*
<i>Willemia intermedia</i>	-.16030	.21261*
<i>Dicyrtoma fusca</i>	.15880	-.19572*
<i>Orchesella cincta</i>	.10275	-.18635*
<i>Pesudachorutus subcrassoides</i>	-.12158	.17014*
<i>Metisotoma grandiceps</i>	.14757	.15498*
<i>Sminthurus sp 2</i>	.07500	-.14793*
<i>Hypogastrura loricata</i>	-.00084	.14626*

* denotes largest absolute correlation between each variable and any discriminant function

Tullbergia granulata (negatively) and *Sminthurinus henshawi* and *Isotoma hiemalis* (positively). FD60 forest separated from other two forests on the basis of function 2. Thirty four Collembola species showed association with Function 2 with *Willowsia buski*, *Neamra muscorum* (negatively), and *Tomocerus minor*, and *Willemia intermedia* (positively) having significant values on this function.

3.5.2 FE Sites

3.5.2.1 Vertical Distribution of Collembola

The total number of Collembola collected in the upper halves of samples from FE forest were higher than those of the lower halves on each sampling date with about 75-80% of the total number of Collembola collected from the upper half (Fig 26). There was little seasonal variation in the percentage of total Collembola occurring in the lower halves of the samples.

3.5.2.2 Total Numbers of Collembola

The FEO areas had higher density of Collembola than either FE40 or FE60 areas and lowest densities were in the FE40 area (Fig 27). Mean densities varied between 389.8-572.0/1000 cm³ in the FEO area, 211.6-357.1/1000 cm³ in the FE40 area, and 209.0-549.0/1000 cm³ in the FE60 area (Appendix A). The mean densities of Collembola increased from July to August in the FEO area, but decreased in FE40 and FE60 areas (Fig 27), but these differences were not significant.

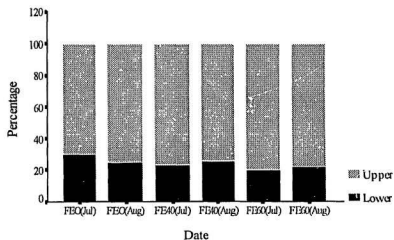


Figure 26. Percentage of the total number of Collembola collected in the upper and lower halves of samples in the FE forest, summer 1994.

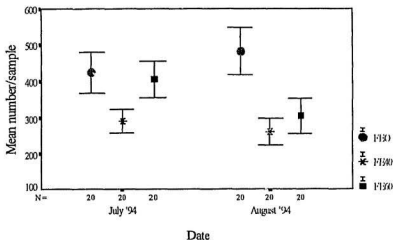


Figure 27. Mean and standard error of the number of specimens of Collembola per sample collected in the FE forest, summer 1994.

3.5.2.3 Faunal Composition

Folsomia penicula was the most abundant species collected in the FE forest, comprising between 20 to 50% of the total number of Collembola (Fig 17, Appendix A). *Isotomiella minor* was the second most abundant species and *Isotoma notabilis*, *Isotoma trispinata*, *Neelus minimus* and *Onychiurus affinis* were also collected in large numbers. The less common species constituted a relatively large portion of the fauna in each of the 3 areas. *Folsomia penicula*, *Isotomiella minor*, and *Isotoma notabilis* were most abundant in the FEO area whereas *Isotoma trispinata*, *Neelus minimus*, *Micrisotoma achromata* and *Isotomurus* occurred in highest numbers in FE40 and FE60 areas. *Isotomurus palustroides*, *Neelus minutus* and *Neelus incertus* were collected only in FE forest.

3.5.2.4 Diversity Indices and Evenness

Diversity of Collembola species as indicated by Shannon-Weiner diversity index and evenness was highest in the FE40 forest (Table 20). Except the lower half of the samples collected in sites FE0-8 (July & August), FE40-9 (July), FE60-11 (July), and FE60-12 (August), all other samples had higher diversity and evenness in the upper halves than in lower halves. The highest diversity index (4.1) and evenness (0.83) were in site FE40-9 in August 1994, and the lowest values (diversity index - 1.4, and evenness - 0.23) were obtained in site FE60-11 in August 1994.

3.5.2.5 Rarefaction

Rarefaction curves for the total number of Collembola collected in all six sites of the

Table 20. Shannon-Weiner diversity indices for Collembola in the upper and lower halves of the soil samples collected from three different aged FE forest, summer 1994.

Area Date, Site	Layers	# Specimens (#Species)	Shannon-Weiner Index	
			H'	Evenness
FEO				
July '94				
FEO-7	Upper	3097 (37)	2.7	0.52
	Lower	823 (24)	2.6	0.56
FEO-8	Upper	3543 (41)	3.2	0.60
	Lower	2070 (36)	3.3	0.64
Aug. '94				
FEO-7	Upper	3310 (45)	3.3	0.60
	Lower	979 (24)	3.1	0.68
FEO-8	Upper	4206 (42)	2.8	0.51
	Lower	1514 (42)	3.0	0.60
FE40				
July '94				
FE4O-9	Upper	2049 (33)	3.7	0.73
	Lower	386 (28)	4.0	0.83
FE4O-10	Upper	2571 (37)	3.5	0.68
	Lower	1000 (36)	3.5	0.67
Aug. '94				
FE4O-9	Upper	1870 (43)	4.1	0.76
	Lower	565 (29)	3.9	0.80
FE4O-10	Upper	2583 (42)	3.2	0.59
	Lower	988 (29)	2.9	0.59
FE60				
July '94				
FE60-11	Upper	3007 (28)	3.0	0.63
	Lower	799 (26)	3.5	0.74
FE60-12	Upper	3320 (44)	3.0	0.56
	Lower	1133 (24)	3.0	0.67
Aug. '94				
FE60-11	Upper	2547 (32)	3.3	0.66
	Lower	943 (27)	1.4	0.23
FE60-12	Upper	1814 (39)	3.2	0.61
	Lower	280 (22)	3.3	0.74

FE forest are given in Fig 23. The highest expected number of species per given sample size was observed in FEO. With smaller sample sizes (less than 2000) the expected number of species generally differed little between sites except site FE60-11 had notably low diversity.

3.5.2.6 Principal Components Analysis (PCA)

Principal Component Analysis separated sites FEO-7 and FEO-8 from other sites of the FE forest whereas the other 4 sites within areas FE40 and FE60 clustered together (Fig 28). FEO-8 was separated from other sites on the basis of factor 1 and site FEO-7 was separated from the rest of the sites on the basis of factor 2. Factor 1 accounted for 34.5% of the overall variation and factor 2 accounted for 22% of the variation among the data (Table 21). Sixteen species had high positive loadings on factor 1 whereas factor 2 had 2 species with high negative loadings (*Isotoma trispinata* and *Neelus minimus*) and 6 Collembola species with positive loadings (Table 21).

3.5.2.7 Discriminant Function Analysis

Discriminant Function Analysis separated areas FE60, FEO and FE40 (Fig 29) with one hundred percent correct classification (Table 22). Twenty nine species showed high association correlation on Function 1 (Table 23) with negative significant correlation values for *Isotoma* sp 1, *Dicyrtoma fusca* and *Willemia denisi*. FE60 separated from other 2 areas on the basis of this function (Fig 29). Function 2, which had 5 species, *Sminthurus henshawi*, *Isotoma manitobae*, *Metisotoma grandiceps*, *Neamira muscorum* and *Isotomurus palustrisoides*, showing significant correlation, separated sites of all 3 ages of forests from each

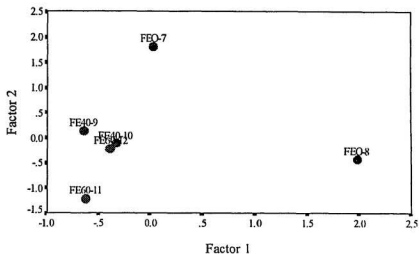


Figure 28. Principal Component ordination of 6 FE sites based on the mean abundance of Collembola over all sampling dates ($n=2$). Collembola species and function loadings are given in Table 21.

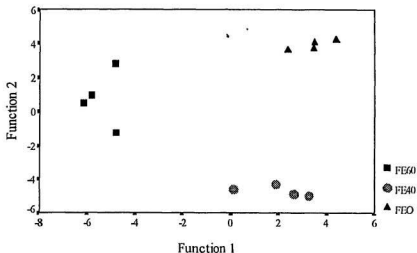


Figure 29. Discriminant function ordination of FE forest sites based on the mean abundance of Collembola in each site on each date. Each point represents mean sample values on a given sampling date. Collembola species and function correlations are given in Table 23.

Table 21. Loadings of Collembola species on the first two factors extracted by Principal Component Analysis in FE study sites

Collembola species	Factor 1	Factor 2
<i>Hypogastrura humi</i>	.99679	-.03267
<i>Tomocerus flavascens</i>	.99436	-.05832
<i>Pseudachorutus subcrassoides</i>	.99015	.05639
<i>Onychiurus paro</i>	.98928	-.11086
<i>Folsomia penicula</i>	.95998	-.11616
<i>Anurida furcifera</i>	.92267	-.30835
<i>Tullbergia granulata</i>	.91845	-.09094
<i>Isotoma ekmani</i>	.90231	-.20518
<i>Isotomurus</i> sp	.88570	.44142
<i>Micrisotoma achromata</i>	.88139	.27585
<i>Onychiurus similis</i>	.88101	.43616
<i>Isotoma manitobae</i>	.87632	.05801
<i>Metisotoma grandiceps</i>	.82869	-.51238
<i>Isotoma beta</i>	.77650	.53798
<i>Stenogastrura hiemalis</i>	.77650	.53798
<i>Tomocerus</i> sp 1	.62340	.32546
<i>Dicrytoma fusca</i>	-.09402	.96602
<i>Sminthurides lepus</i>	-.00678	.92443
<i>Hypogastrura loricata</i>	.13869	.91654
<i>Pseudachorutus aurofasciatus</i>	-.01119	.90073
<i>Lipidocyrtus cyaneus</i>	-.14253	.89907
<i>Isotoma trispinata</i>	-.28373	-.87322
<i>Isotoma hiemalis</i>	-.12870	.81650
<i>Neelus minimus</i>	-.42098	-.76946
% Variance explained	34.5%	22.5%

Table 22. Classification results of the Discriminant Function Analysis from the FE forest.

Actual Group	No. of Cases	Predicted Group Membership		
		1	2	3
Group 1 (FEO)	4	4 100.0%	0 .0%	0 .0%
Group 2 (FE40)	4	0 .0%	4 100.0%	0 .0%
Group 3 (FE60)	4	0 .0%	0 .0%	4 100.0%

Percent of "grouped" cases correctly classified: 100.00%

Table 23. Summary table of Collembola species showing highest on Discriminant Functions 1 and 2 of FE study sites (significant value for 95% confidence level is 0.53 when n=12).

Species	Function 1	Function 2
<i>Isotoma sp 1</i>	-.66827*	.02512
<i>Dicyrtoma fusca</i>	-.61413*	.14502
<i>Willemia denisi</i>	-.53523*	.01437
<i>Neelus minimus</i>	.51728*	.38893
<i>Isotomurus sp</i>	.50222*	.12743
<i>Isotoma notabilis</i>	.38530*	.19233
<i>Tomocerus minor</i>	.37148*	.36159
<i>Sminthuridus lepus</i>	-.36966*	.17956
<i>Pesudachorutes aureofasciatus</i>	-.36836*	.13070
<i>Tomocerus sp</i>	.35925*	.06223
<i>Sminthurus henshawi</i>	.18018	.87963*
<i>Isotoma manitobae</i>	.17754	.83337*
<i>Metisotoma grandiceps</i>	.30356	.67461*
<i>Neanura muscorum</i>	-.00953	.62439*
<i>Isotomurus palustroides</i>	.31563	.60870*
<i>Neelus minutus</i>	.36746	.47112*
<i>Isotomiella minor</i>	-.21182	.46082*
<i>Onychiurus similis</i>	.36948	.42644*
<i>Orchesella cincta</i>	.09462	.34509*
<i>Neelus incertus</i>	.07726	.33960*
<i>Isotoma hiemalis</i>	.11933	.30146*

* denotes largest absolute correlation between each variable and any discriminant function

other at equal distance.

3.5.3 Comparison and Classification of Soil Samples

3.5.3.1 Cluster Analysis

Results of the cluster analysis for species abundance data in soil samples from both FD and FE forests are summarized in Figure 30. A grouping of different aged forests and habitats with sampling dates indicated by 2 main clusters can be observed in this dendrogram. Cluster 1 mainly made up of samples from FDO, FD60 and FE forests, and Cluster 2 was made up of samples collected from areas FD40 and FDO. Cluster 1 can be further divided into 2 subclusters; cluster 3 and 4. Subcluster 3 was made up primarily from the samples collected in FDO 1992, FD60 1992 and 1993. This cluster also had samples from area FD40 collected in July 1992. Subcluster 4 was composed of samples collected from the FE forest.

Cluster 2 also has two subclusters, cluster 5 and 6. Subcluster 5 was characterized by samples collected from area FD40 in 1993 and Cluster 6 had samples from area FDO collected in 1993 and 1994. Samples from area FD60 JUN94 and FD40 AUG92 were relatively distinct and were grouped with other clusters at a low level of similarity.

Results of the cluster analysis for the presence/absence data for the soil, pitfall and microhabitat samples are given in Figure 31. The two main clusters recognized here represent pitfall and microhabitat samples (cluster 1) and soil samples (cluster 2). Cluster 1 can be

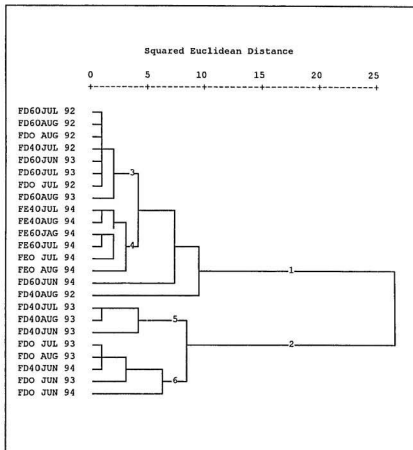
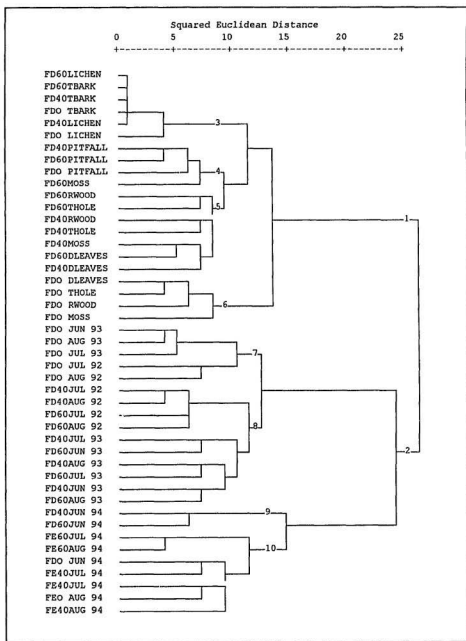


Figure 30. Dendrogram of Cluster Analysis of quantitative data of Collembola species abundance in soil samples from FD and FE forests. Squared Euclidean distance coefficient and group average linkage clustering methods were used. (Sample name: first 3/4 letters indicate the site name; next 3 letters indicate sampling month: Jun-June; Jul-July; Aug-August; last 2 numbers indicate year 92-1992; 93-1993; 94-1994).

Figure 31. Dendrogram of Cluster Analysis of presence/absence data of Collembola collected from soil samples, pitfall traps, and microhabitat samples from FD forests. Squared Euclidean distance coefficient and Group Average Linkage clustering method were used (For the soil samples: first 3/4 letters indicate site name; next 3 letters indicate sampling month: Jun - June, Jul - July, Aug - August; last 2 numbers indicate year 92- 1992; 93- 1993; 94 -1994. For microhabitat samples: first 3/4 letters indicate site name and the rest indicate the type of microhabitat: Lichen-lichen from live and dead trees, Tbark-bark from live and dead trees, Moss- moss from live and dead trees, Rwood- rotten wood, Thole- tree hole, Dleaves- deciduous leaves. Pitfall trap samples are indicated by site name following PITFALL).



divided into 4 subclusters: cluster 3 entirely composed of microhabitat samples collected from trees from all 3 areas; cluster 4 composed of pitfall trap samples; cluster 5 containing samples collected from the ground in FD40 and FD60 areas; and cluster 6 has ground samples from the FDO area. Within the second major cluster (2), the principal groups are: cluster 7 composed of samples collected from the FDO area in 1992 and 1993; Cluster 8 containing samples collected from regrowth sites in 1992, 1993; Cluster 9 composed of samples collected from FD40 and FD60 areas in 1994; and cluster 10 containing samples collected from the FE forest as well as samples from the FDO area June 1994.

3.5.3.2 Two Way Indicator Species Analysis (TWIN SPAN)

The flow-chart of the Two Way Indicator Species Analysis showing the classification of the sites and the indicator species of Collembola responsible for this classification is given in Figure 32 and the two-way table of the classification is given in Appendix C. The first division in Figure 32 shows the separation of FE and FDO sites from FD40 and FD60 sites. The positive indicator species for FE and FDO are *Isotoma* sp 3, *Tomocerus* sp, *Arrhopalitus benitus* and *Isotomurus* sp. The second division separated the FE from FDO sites with the indicator species for FE being *Neelus incertus* and *Friesea alaskella* whereas *Stenogastrura hiemalis* characterized the FDO sites. Seasonal variation in the presence of Collembola species in FD40 and FD60 forests was associated with the 3rd division of the flow chart. *Neelus minimus*, *Orchesella cincta*, *Arrhopalitus hirtus* and *Willemia denisi* were the positive indicator species for the early summer and *Isotoma manitobae*, *Isotoma viridis* and *Tomocerus minor* are the positive indicator species for the late summer samples.

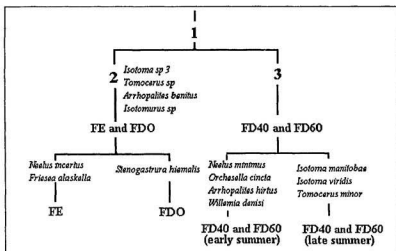


Figure 32. Flow chart of the results of TWIN SPAN analysis of the Collembola species collected from both FD and FE forests, 1992 to 1994.

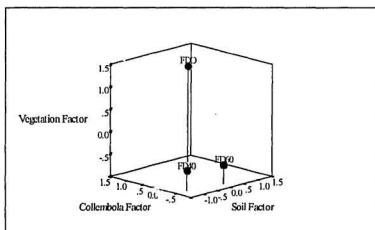


Figure 33. Principal Component ordination of the 3 different aged FD forests based on vegetation, soil characteristics and the abundance of Collembola species.

3.6 Relationship Between Collembola Communities and Ecological Factors

Mean values for the FD forest over the entire study period were plotted against factor I of each of the PCA analysis of vegetation, soil and Collembola communities of the FD forest in a 3D scatterplot to examine the relationship between ecological factors and Collembola communities (Fig 33). In this graph each point represents the mean value of each character for the whole sampling period. Area FDO was separated from FD40 and FD60 on the basis of both Collembola and vegetation factors. All three aged forests were separated in equal distance on the basis of soil factor.

3.7 Ecology of The Collembola Species

The general ecology of each of the 61 species of Collembola collected from the study sites is given here. The purpose of this section is to present observations on aspects of the ecology of each species of collembolan collected as well as to provide an overview of its geographical distribution (* - indicates no published records are available on the distribution except in North America) . The order of species accounts follows Table 12.

Family - Hypogastruridae

Hypogastrura (Mitchellania) loricata

This species was common in the pitfall traps at all six FD sites. It also was collected in soil samples, most abundantly in FD40 area. Abundance of this species was generally low in the FE and FD60 sites. This species was also collected in microhabitat samples from the ground and a few were in lichens from live and dead trees.

Distribution: Nearctic (Christiansen 1990).

Hypogastrura (Hypogastrura) humi

A common euedaphic species collected in both FDO and FEO areas but was absent from some of the 40 year and 60 year old sites. This species was collected rarely in the pitfall traps (in FDO and FD60 areas) and in microhabitats (in tree hole, rotten wood, deciduous leaves and moss samples).

The results of PCA showed that this species was abundant in FEO and FDO areas.

Distribution: Nearctic (Christiansen 1990).

Stenogastrura hiemalis

This species was collected in soil samples from FDO and FEO areas in summers 1993 and 1994, and in deciduous litter and moss samples from the FDO area.

PCA showed that this species occurred in FEO and FDO areas and TWINSpan also indicated that this was present in the FDO area.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Willemia denisi

This is one of the rare euedaphic species. It was evenly distributed among different sites but occurred in low abundance. This species was also collected in the microhabitat samples from the ground.

This species was indicated by TWINSpan as found more abundantly in FD40 and FD60 areas in early summer.

Distribution: Holarctic (Christiansen and Bellingner 1980).

Willemia intermedia

This species was found in low numbers in all 12 sites in both soil and ground microhabitat samples. Highest abundance of this species was observed FD40 and FDO areas in summer 1993.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Friezea sublimis

A deep soil dwelling species that was present in low numbers in most of the sites. This species was found in highest numbers in the FD60 area, and rarely in the microhabitat samples from the ground, at all FD forests.

Distribution: Holarctic (Marshall 1967).

Friezea alaskella

This species was collected primarily in the soil samples from the FE forest and it was most abundant in FE40 area. A few specimens were also collected from FD forest, 1994.

TWINSPAN analysis indicated that this was most abundant in the FE forest.

Distribution: Nearctic (Fjellberg 1985).

Pseudachorutes subcrassoides

This euedaphic species was rare but present in all sites of both FD and FE forests. This species is significant in both Discriminant Functions Analysis (DFA) and PCA in both FD and FE forests.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Pseudachorutes aureofaciatus

This species was most common in the pitfall trap samples. It also occurred in some

of the soil samples from FD and FE forests.

PCA showed that this species was most abundant in the FEO-7 site.

Distribution: Nearctic (Marshall 1967).

Amurida pygmaea

This tiny, euedaphic, species was collected only from the soil samples. It was present in small numbers at all sites.

Distribution: Holarctic (Kaczmarek 1975).

Amurida furcifera

This species was collected only from the soil samples. It was present in small numbers at all sites. This species was most abundant in the FE forest.

PCA indicated that this was most abundant in the FEO area.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Neanura muscorum

This epedaphic species occurred mainly in the pitfall trap samples but a few specimens were also collected in the soil and microhabitat samples from the ground. Although it was found in all 12 sites, highest abundance was observed in the FD60 area.

The results of DFA indicated that this species was more abundant in area FD60, FEO and FE40 areas and PCA showed that this was abundant in the FD forest.

Distribution: Cosmopolitan (Marshall 1967, Goddard 1972, Chernova *et al* 1973).

Family : Onychiuridae

Onychiurus (Protaphorura) similis

Onychiurus similis, an euedaphic Collembola, was collected only in soil samples and microhabitat samples from the ground (rotten wood, tree hole, deciduous leaves, and moss). It occurred in all sites on all sampling dates. It was not abundant in the FDO and FEO sites but was found in high numbers in the FD60 area in June 1994.

*Distribution: Nearctic (Christiansen and Bellinger 1980).

Onychiurus (Onychiurus) paro

Onychiurus paro, one of the most abundant species in both forest types, was collected in soil samples from all 12 sites and also occurred in tree hole, rotten wood, deciduous leaves and moss samples. This collembolan was abundant in FDO and FD40 areas.

*Distribution: Nearctic (Christiansen and Bellinger 1980).

Onychiurus (Archaphorura) affinis

This euedaphic species was generally more abundant in FE than FD sites but was also collected in high numbers at FDO-2, June 1993. This species was also common in the same microhabitat samples where other two *Onychiurus* species were found.

Distribution: Holarctic (Kaczmarek 1977).

Tullbergia (Tullbergia) granulata

This was one of the most abundant euedaphic Collembola in the FD forest and was also collected in considerable numbers in the FE40 and FEO areas. This species was collected in very low numbers from deciduous leaves (in FDO and FD60 areas), tree hole and moss samples (in the FD60 area).

The results of PCA showed that this species occurred in higher numbers in FD40, FD60 and FEO areas.

*Distribution: Nearctic (Christiansen and Bellinger 1980).

Family - Isotomidae

Uzelia setifera

This species was collected only in the microhabitat samples from tree bark and lichens and mosses on trees.

Distribution: Holarctic (Christiansen and Bellinger 1980).

Amurophorus binoculata

Amurophorus binoculata occurred in low numbers in the soil samples in all 12 sites.

Distribution: Holarctic (Usher 1970).

Folsomia penicula

Folsomia penicula was the most abundant species in all 12 sites on all sampling dates except in the FD40 area in 1992. It made up 50 - 60 % of the total number of specimens collected in each site. Highest abundance occurred in the FDO area in summer 1993. This was also the dominant species in microhabitat samples collected from the ground.

PCA indicated that this species was more abundant in both FDO and FEO areas.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Metisotoma grandiceps

A common species found in highest numbers in the old forest sites but was also present at the regrowth sites of both FD and FE forests. This species was also collected rarely in the pitfall traps and in microhabitat samples (rotten wood, deciduous leaves and moss samples) in all six sites of the FD forest.

The results of PCA indicated that this species was abundant in FDO and FEO areas and the results of DFA showed that this collembolan was also abundant in FEO and FE40 areas.

*Distribution: Nearctic (Christiansen and Bellinger 1980).

Micrisotoma achromata

This species was collected only in the soil samples and was present in all 12 sites. Highest abundance of this species was found in the FE forest.

PCA indicated that this was more abundant in the FEO area.

*Distribution: Nearctic (Christiansen and Bellinger 1980).

Isotomiella minor

This was the most abundant species in area FD40 in 1992 and the second most abundant species in remaining sites in both FD and FE forests. It was collected in higher numbers in regrowth sites than in the old forest. This species was also found abundantly in microhabitat samples from the ground.

Distribution: Cosmopolitan (Marshall 1967, Nijima 1971, Chernova *et al* 1973, Mitra *et al* 1977).

Isotomurus sp

This is an epedaphic form mostly collected in the pitfall trap samples although some specimens were also collected in soil samples. Highest abundance was observed in FDO, 1993 and 1994, and in FE60 areas, August 1994. This species was present at other sites in lower numbers.

It was indicated by TWINSpan analysis that this *Isotomurus* sp was more abundant

in both FDO and FEO areas and PCA showed that it was most abundant in FE and FDO areas.

Isotomurus pulvustroides

This species occurred only in the FEO and FE60 areas. The abundance was highest in FE60 area in August 1994.

DFA indicated that this was more abundant in the FE forest.

Distribution: Cosmopolitan (Danks 1981).

Isotoma ekmani

Isotoma ekmani, a rare species, was collected in soil samples from sites FDO-1, 1993 and FE40-10, August 1994.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Isotoma notabilis

This was one of the most abundant species in both FD and FE forests and was collected in soil and microhabitat samples from ground. Highest abundance in soil samples occurred in the FDO area in summers 1993 and 1994 but considerable numbers were also collected from the FD40 and FD60 areas on the same sampling dates.

Distribution: Cosmopolitan (Chernova *et al* 1973, Stebayeva 1975).

Isotoma trispinata

This was one of the most abundant species collected in the FE forest. Highest abundances were recorded in FEO-8 and FE60-12 sites. This species was also collected in high numbers in the FD forest in both soil and microhabitat samples from the ground.

PCA showed that it was abundant in the FE60 area.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Isotoma manitobae

This was a common species found in the FE and FDO forests. Highest abundance of this species was observed in FE40 area. A few specimens were collected at the FD40 and FD60 areas, 1992 and 1993. This species was also collected in the microhabitat samples from the ground in FDO forest.

TWINSPAN indicated that this was more abundant in late summer in FD40 and FD60 areas. Also the results of DFA showed that this was more abundant in FE40, FEO, FD40 and FDO areas.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Isotoma hiemalis

A common species found in FEO and FE40 areas, this species was also found in low numbers in the FDO area. This species was also collected in the microhabitat samples from the ground in FDO and FD60 areas.

The results of PCA showed that this was more abundant in FEO-7 and FDO forests.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Isotoma viridis

This species was collected in low numbers in soil and microhabitat samples (from the ground and in lichens from dead and live tree) from most sites. It is an epedaphic form and was common in pitfall trap samples in FDO and FD40 areas.

TWINSPAN analysis indicated that this was abundant in FD40 and FD60 areas in late summer.

Distribution: Holarctic (Goddard 1972).

Isotoma beta

This was a very rare species and found only in the FDO-2 site, 1992.

ICA indicated that this was more abundant in the FDO area.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Isotoma spp.

Eight unidentified *Isotoma* (*Desoria*) spp were collected from the 12 sites from soil, pitfall and microhabitat samples. Most of these species were rare and occurred only at one or two sites on one or two sampling dates. Species 1-5 were collected from soil and microhabitat samples from the ground and species 6-8 were found only in the pitfall traps.

The results of DFA showed that species 1 was more abundant in the FE60 area and PCA indicated that species 2-5 were more abundant in the FDO area. Also TWINSpan analysis indicated that species 3 was more abundant in FE and FDO forests .

Family: Entomobryidae

Orchesella cincta

This is an epedaphic form collected primarily from 40 and 60-year-old FD and FE forests. A few were also collected from FEO area. This was the dominant species in the pitfall traps collected in FD40 and FD60 areas and a few adults and immature forms were collected in the soil and microhabitat samples (tree hole, rotten wood, deciduous leaves and moss samples) in the same sites.

TWINSpan analysis indicated that this species was more abundant in FD40 and

FD60 areas in early summer.

Distribution: Holarctic (Stach 1966).

Entomobrya multifasciata

A common epedaphic species collected in all 12 sites of both FD and FE forests. This was one of the most abundant species collected in the pitfall traps from the six sites of the FD forest. This species was also collected in considerable numbers in microhabitat samples from the ground and the trees.

Distribution: Cosmopolitan (Chernova *et al* 1973).

Entomobrya nivalis

This epedaphic species was collected only in the pitfall trap samples in the FDO area.

Distribution: Holarctic (Goddard 1972).

Entomobrya comparata

This species was collected only in the pitfall traps in all FD forests.

Distribution: Holarctic (Danks 1981).

Willowsia buski

Willowsia buski is an epedaphic species that was collected in low numbers in all three types of samples from the regrowth areas. The highest abundance was recorded at the FD60 area, 1993.

The results of DFA showed that this was more abundant in the FD60 area and PCA showed that this was more abundant in the FD forest.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Lepidocyrtus cyaneus

This was a rare species collected in soil samples from the following habitats: FDO-1 and FDO-2, 1993; FD60, 1992; and FEO-7 and FE40-9, 1994. It was also collected in pitfall traps in FD60 area and in moss and deciduous litter in FDO and FD40 areas.

PCA indicated that this was more abundant in FD60-6 and FEO-7 sites.

Distribution: Cosmopolitan (Stach 1966).

Tomocerus flavescens

This is an epedaphic form of Collembola found in high numbers in pitfall traps in the FDO are. A few adults and immatures were also found in the soil and microhabitat samples (from ground and trees) collected from both FDO and FEO areas.

PCA showed that this species was more abundant in FDO and FEO forests.

Distribution: Cosmopolitan (Danks 1981).

Tomocerus minor

This is an epedaphic species restricted to regrowth FD and FE forests. Adults and immature forms of this species were also found in the pitfall samples.

The results of DFA showed that this was most abundant in the FD40 area and TWINSpan analysis indicated that this species was most abundant in late summer in the FD40 and FD60 areas.

Distribution: Cosmopolitan (Stach 1966).

Tomocerus sp.

This species was found commonly in the microhabitat samples both from the ground and trees and also collected in low numbers in all 3 ages of both FD and FE forests in 1993

and 1994.

TWINSPAN analysis indicated that this species was most abundant in FE and FDO forests. Also PCA showed that this was most abundant in FDO and FEO areas.

Family: Neelidae

Neelus minimus

This common species was collected in the soil samples from all 12 sites. It was most common in the FE forest and the highest abundance was recorded in the FE60 area.

The results of PCA showed that this collembolan was most abundant in the FE60-11 site. TWINSPAN indicated that this was abundant in early summer in the FD40 and FD60 areas.

Distribution: Cosmopolitan (Mitra *et al.* 1977, Poole 1961).

Neelus minutus and *N. incertus*

These two species were only collected in the FE forest where they occurred in all sites except FEO-7.

TWINSPAN analysis indicated that *N. incertus* was most abundant in the FE forest
Distribution: Cosmopolitan (Marshall 1967).

Family: Sminthuridae

Sminthurides lepus

The highest abundance of this species was in the FDO area, 1994, although it was commonly found at all 12 sites. This species was also collected in microhabitat samples from

the ground.

PCA indicated that this species was most abundant in FDO and FEO areas.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Arrhopalites hirtus, *A. benitus* and *A. diversus*

These epedaphic species were collected in very low numbers in all sites. These were also collected in the microhabitat samples from the ground.

TWINSPAN analysis indicated that *A. benitus* was most abundant in FE and FDO forests and *A. hirtus* was found more abundant in FD40 and FD60 areas in early summer. Also PCA showed that *A. benitus* was most abundant in the FDO area.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Sminthurinus quadrimaculatus

The abundance of this species was very low, but it was collected in all 12 sites in the soil samples and rarely in the microhabitat samples. This was also collected in the pitfall traps in the FD60 area.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Sminthurinus henschawi

This is an epedaphic form collected in low numbers in FDO, FD60 and FE60 areas. This species was also collected rarely in the microhabitat samples from the ground.

The results of PCA showed that this species was most abundant in FDO areas.

*Distribution: Nearctic (Christiansen and Bellingner 1980).

Sminthurus sp. 1 and 2

These species occurred in all 12 sites but were collected in very low numbers. They

were absent from the regrowth sites in 1992.

PCA showed that both species were abundant in FDO area.

Dicyrtoma fusca

This epedaphic Collembola was collected in soil and microhabitat samples from FD40 and FD60 areas and was also collected in the soil samples from the FE forest.

DFA indicated that this species was most abundant in the FE60 area and PCA showed that this was most abundant in the FEO area.

Distribution: Holarctic (Goddard 1972).

Dicyrtoma (Ptenothrix) spp.

Three *Ptenothrix* spp. were collected in high numbers in pitfall traps in both FD40 and FD60 areas. Species 1 was also found in the pitfall traps in the FDO area.

4. DISCUSSION

4.1 Habitat Characteristics in Different Aged Forests

The soil of the FD forest is classified as a Ferro-Humic Podzol characterized by having a 10 cm Bhf horizon with a high organic matter content. A considerable amount of iron and aluminium also found here gives a reddish brown colour to the soil (Meades and Moores 1989). During the developmental process of the soil, especially in podzolic soils, most of the available bases, such as iron and lime, will be removed by leaching and accumulate at two or three feet below the surface (Pearshall 1968). This might be the reason for the declining of the concentration of some inorganic substances, for example aluminium, ash and iron, with forest age in FD forest sites. The development of the vegetation also is normally accompanied with soil development. Organic materials accumulate as the roots die and aerial organs of plants fall as litter. This explains the higher amount of organic substances and carbon in FDO than FD40 and FD60 forests.

Both Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA) showed the above mentioned differences in soil characters between FD forests of different ages, although most characteristics were similar and did not show any patterns between age classes. The soil of all three ages of FD forest was very acidic.

Balsam fir forest of Newfoundland is a simple forest type, low in diversity of overstorey and understorey plant species. Like most boreal forests balsam fir is a disturbance-driven forest. Tree density, small tree density, shrub density, shrub diversity and foliage

diversity increased from FD40 to FD60 areas probably because the relatively large open canopy permitted a well developed understorey vegetation. Forest structure changed markedly from FD60 to FDO, largely as a result of mortality among small trees and shrubs. Both PCA and DFA clustered FD40 and FD60 areas together and separated the FDO area from them indicating that the old forest has some different floral conditions than the younger forests. As the forest gets older the canopy blocks more light which restricts understorey vegetation. Reduced understorey vegetation in the old forest is also associated with the increasing organic matter in the soil.

The overall results of the analysis on habitat characteristics show that clear-cutting does have a major effect on vegetation parameters especially in the diversity and density of understorey and overstorey vegetation. But the soil variables do not show a pattern with different aged forests except in amounts of some inorganic substances and organic matter of the soil.

4.2 Collembola Community Structure in Balsam Fir Forests

4.2.1 Collembola Fauna in Different Microhabitats

Among the 29 genera and 61 species of Collembola identified in this study from balsam fir forest, 7 genera and 7 species had been reported previously from Newfoundland by Stach (1966). The remaining 22 genera and 54 species are new Newfoundland records. Species composition within samples collected from pitfall trap (22 species), microhabitats (38 species) and soil samples (61 species) differed, indicating these techniques sampled different

associations of collembolan species.

The primary division in the Cluster analysis of collembolan species presence/absence data separated soil samples from combined pitfall trap and microhabitat samples. The pitfall trap samples were grouped together with the ground microhabitat samples indicating that the Collembola diversity was similar in both types of samples. This was because most of the Collembola collected by these sampling methods were large, surface-living species whereas most of the Collembola in the soil samples were small, deep soil dwellers. This supports Mitchell (1979) who reported that soil arthropod body size decreases with depth due to space limitations and the lowered chance of dehydration.

Pitfall trap samples from forests of different ages did not differ, indicating a similar soil surface fauna across the three ages of forest. Among the microhabitat samples, the Collembola species associations collected from trees differed from those of the ground. *Uzelia setifera* was found only in the lichens and bark of both live and dead trees. *Entomobrya multifasciata* and *Tomocerus flavescens* which have been recorded from superficial layers of the litter and on surface vegetation (Poole 1961 and Vegter *et al.* 1988), were also found on trees.

The qualitative data of Collembola species collected in different microhabitats (Tables 14-16) showed the variation in the presence of each species in different aged forests. Number of Collembola species increased from FD40 area (27 species) to FDO area (35 species). These

results show that clear cutting does have an effect on the diversity of Collembola in different microhabitats in the FD forest habitat (Tables 14, 15 16). The old forest has the highest diversity, indicating that as the forest age increases so does the diversity of Collembola.

4.2.2 Collembola fauna in Different Forests

4.2.2.1 Vertical Distribution

Collembolan abundance and diversity decreased with increasing soil depth. On average, about 60-75% (in FD forest) and 75-80% (in FE forest) of the total Collembola population occurred in the 0-5 cm depth zone. Similar patterns have been reported in other forests (Poole 1961, Nijima 1971, Price 1973, Huhta *et al.* 1986, and MacLean *et al.* 1977). The majority of Collembola collected in the soil samples were euedaphic springtails of relatively small size. Probably the reason for the higher density, especially in the FE forest, of Collembola in the upper layers is that their ability to migrate downwards into the soil is limited by the rapid decrease in size of soil pores and increase in water logging with increasing depth (Christiansen 1990). Also, fungi, the main collembolan food are probably quantitatively and qualitatively more abundant in the upper layer of the soil than the deeper layer. However, *Tullbergia granulata* was more abundant in the lower 5-10 cm layer suggesting it may avoid warmer surface soil temperatures and prefer more humid wet soil conditions. A congeneric species, *Tullbergia kraushaueri*, has been reported to show this preference in pine forest and other coniferous forest soil (Poole 1961, Kaczmarek 1975).

A seasonal pattern was observed in FDO and FD40 areas in the proportion of

Collembola occurring in the lower half of the samples. In late summer the proportion of Collembola in the lower halves of samples was higher than that of the early summer. Huhta *et al.* (1986), in Finish coniferous forests, found a late summer increase in the total numbers of Collembola in the deeper layers over that of spring and early summer. Apparently some Collembola moved downwards in the soil to avoid drought and extremes of temperature (Christiansen 1964, Jooisse and Verhoef 1974). These patterns were not observed in the FD60 area which is a moister site and therefore drying and high temperatures would have less effect on Collembola in the upper layers. Stebayeva (1975), in his study of phytogenic microstructure of Collembola associations in steppes and forests of Siberia, reported that maximum density of Collembola occurred in litter when soil moisture was high. However, when the soil was very warm, Collembola were practically absent in the upper (0-5 cm) layer, but occurred in large numbers in the deeper soil layers (5-10 cm) where soil moisture was higher.

Although the total number of specimens and species were higher in the upper 0-5 cm layer, the values of Shannon-Weiner diversity indices and evenness were higher in the lower layers in some samples. This apparent contradiction is attributed to the fact that although the lower layers had fewer specimens, a similar number of species were present so that distribution of specimens among species was more even. Diversity indices are useful to characterize species abundance relationships in communities (Ludwig and Reynolds 1988). Higher values of diversity indices usually mean that those samples are more diverse with higher total numbers than other samples. That the results of this study did not support this

statement may be because diversity indices often attempt to incorporate both numbers of species and evenness into a single numerical value. Different authors use different indices to measure diversity, and the whole subject area has become somewhat confused with poor terminology and an array of possible measures (Krebs 1989, Ludwig and Reynolds 1988). As this study is not based on the mathematics of the diversity indices, I would not like to make any conclusions regarding diversity indices.

The proportion of Collembola in the upper halves of the FE samples was consistently higher than that of the FD habitat. The FE forest is wetter and has a hard, packed, muck layer below the humus layer with less pore size which supports very low numbers of Collembola. The upper humus layer remained moist throughout the summer, protecting Collembola from drying so that most of the specimens stayed in the upper layers throughout the year.

4.2.2.2 Total Abundance

Collembola may be present in large numbers in forest soils. During mass emergence or swarming, estimates of over 1 million/m² have been reported (Marshall *et al.* 1990). Reported population densities in different forest habitats vary widely. The mean densities of Collembola in Newfoundland balsam fir forest varied between 17,440-84,881 m⁻² (in FD) and 27,740-48,820 m⁻² (in FE). These densities are within ranges of most of the numbers previously reported from various forest habitats in USA, Canada and Europe (Table 24). Higher density estimates are generally obtained when a high gradient extractor is used rather

Table 24. Densities of Collembola in different forests soils from published records and the present study.

Author	Habitat & Locality	No./m ³ (in thousands)	No./cm ³ (sample depth-cm)
Poole (1961)	coniferous forest, North Wales	46	—
Bchan (1972)	spruce mor, Ontario	160	3.2 (5)
Vlug & Borden (1973)	coniferous forest, British Columbia	22.61	0.2261
Price (1973)	pine forest, California	44	
Kozemurk (1977)	pine forest, Poland	19 - 23	0.38 - 0.46 (5)
Kozemurk (1977)	deciduous forest, Poland	25.1 - 26.5	0.502 - 0.53 (5)
Maclean <i>et al.</i> (1977)	Alaskan Arctic tundra	24 - 180	0.24 - 0.36 (10)
Seastadt & Crossley (1981)	pine hardwood, North Carolina	3.7 - 15	0.27 - 0.3 (5)
Peterson (1982)	coniferous forest, Denmark	3 - 300	—
Peterson (1982) (Lcinass pers. Comm.)	spruce forest, Norway	145 - 244	—
Peterson (1982) (after Mateuzzi 1968)	Evergreen oak forest, Italy	105	—
Bird & Chatarpaal (1986)	conifer hardwood, Ontario	0.3 - 26	3x10 ⁻⁴ - 0.26 (10)
Teuben & Smidt (1992)	pine - mor, Netherlands	27.1 - 29.73	—
Teuben & Smidt (1992)	pine - mull, Netherlands	28.7 - 46.9	—
present study (1992)	fir - mor, Newfoundland	17.4 - 33.9	0.17 - 0.33 (10)
present study (1993)	fir - mor, Newfoundland	24.6 - 69.0	0.24 - 0.69 (10)
present study (1994)	fir-mor, Newfoundland	36.3 - 84.9	0.36 - 0.85 (10)
present study (1994)	fir-mull, Newfoundland	27.7 - 48.8	0.27 - 0.48 (10)

than Berlese funnels. Marshall (1972) stated that efficiency of extraction for Collembola was only 45% with Berlese funnels whereas Bird and Chatarpaul (1986) found 73% efficiency for Collembola with high gradient extractors. Deficiencies in extraction of Collembola would affect samples from each site equally and therefore would not affect conclusions drawn from the data.

The density of Collembola in the FD forest varied over the three years, especially in 1992 when the density was lower than that of the following years. This may have been an artefact of the extraction procedure. Extraction in 1992 was carried out in a small, closed room which resulted in high room temperature (unrecorded but certainly above 20°C) that might have killed some of the Collembola before they could leave the samples. After extraction, the samples were sieved and examined for remaining animals and about 10-20 Collembola/sample were collected. Also some of the specimens in collection jars from the July 1992 samples were damaged by mould because the preservative was too dilute although most could be counted. These might be the reasons for the apparent increase in abundance of Collembola from 1992 to 1993. The total abundance of Collembola was not statistically significantly different from 1993 to 1994.

Seasonal variation was noticed in the total number of Collembola collected in the FD forest. Total abundance was higher in June and August than in July. This midsummer population depression could be related to life history patterns, the effect of drying and warming of the soil or predation (Christiansen 1964). Similar seasonal variation in

collembolan density has been reported in sites where effects of whole-tree and conventional forest harvest have been investigated (Bird and Chatarpaul 1986). These authors suggest dryness and warm temperatures are the principal factors responsible for the population decrease in summer.

4.2.2.3 Diversity of Collembola

The total number of species of Collembola found in this study (61 species), is comparable to those reported from other Canadian and boreal forest faunas. Marshall (1967) reported 36 genera and 58 species of Collembola in Quebec woodland humus; Marshall *et al.* (1990) reported 22 taxa of Collembola in forest nurseries of British Columbia; Huhta *et al.* (1986) reported 15 and 13 species of Collembola from two different coniferous forests in southern Finland; and MacLean *et al.* (1977) recorded 20 Collembola species in Alaskan Arctic tundra. Thus collembolan communities of forest soils are usually diverse.

Two members of the family Isotomidae, *Folsomia penicula* and *Isotomiella minor*, were the dominant species in both forests. Together they comprised about 70% in the FD forest and 50-60% in the FE forest of the total number of Collembola. Similarly, MacLean *et al.* (1977) reported two species, *Folsomia diplophthalma* and *Folsomia quadrimaculata*, comprising 70% of the total number of Collembola in Alaskan tundra.

The diversity and evenness of Collembola were higher in the FE forest than in the FD forest although total numbers were highest in the FD forest. Some Collembola species prefer

moist, cool conditions and require a relative humidity of over 89% (Christiansen 1964). *Orchesella cincta* and *Tomocerus minor*, which were found in considerable numbers in the FD60 area (the wettest site in the FD forest), were more abundant in the FE forest than FD forest. Vegter *et al.* (1988), in their study of distributional ecology of forest floor Collembola (Entomobryidae) in the Netherlands, found that five entomobryid species, including *Orchesella cincta* and *Tomocerus minor*, were most abundant in moist clay habitats. *Isotomurus palustris*, *Neelus minutus* and *Neelus incertus* were collected only in the FE forest. *Neelus minimus* was collected in low numbers in the FD forest but was one of the most abundant species in the FE forest. These six species of Collembola seemed to occupy wetter conditions than the other species collected in balsam fir forests.

Peak populations of the various species tended to occur at different times in a year. Whether these population changes were real or caused by sampling and extraction methods is unknown. However, no regular seasonal population peaks of Collembola have been reported so far. According to Christiansen (1964), patterns of population fluctuation in Collembola vary not only from species to species but from year to year and geographically. Poole (1961) recorded maximum population peaks in August for *Isotomiella minor* and *Isotoma notabilis* in a coniferous forest soil in North Wales. In the present study, *Isotoma notabilis* showed an August peak population in the FE forest and a June peak population in the FD forest. *Isotomiella minor* had an August peak population in the FD forest and a July peak population in the FE forest. Poole (1961) also stated that the whole collembolan community is in a constant state of flux with first one species increasing and then another,

depending on varied environmental factors favouring different species. As little is known of the factors influencing the lives of Collembola, it is difficult to account for population changes based on a single year's data. Pools's (1961) comments might explain the above results but it is obvious that further research on the population dynamics of single species is needed.

Almost all of the species collected from Newfoundland balsam fir forest also occur widely over North America and Europe and some are cosmopolitan. Blackith and Blackith (1975) reported wide distributions for some species of the families Onychiuridae, Entomobryidae and Isotomidae which occur in Asia, Europe and many localities of North America. For example, *Neanura muscorum*, a common species in all 3 types of samples, is widely distributed in North America, Europe, Greenland and North Africa (Goddard 1972).

Marshall (1967) reported that 31% of North American Collembola were Holarctic or cosmopolitan in distribution and 50% of the northern Canadian species were known from Europe. Many of the species found in Newfoundland also have been reported in the Maritime Provinces (Christianson and Bellinger 1980; Stach 1966). Stach (1966) suggested (after Lindroth 1957) that human transport was the primary reason for the presence of so many number of European Collembolan species in Newfoundland. He stated that these species must have been introduced here in older times, when the ballast of sailing vessels from Europe was left behind Atlantic Canadian Provinces. However, given the wide distributions of northern Collembola, this argument seems unlikely. Recent data on Collembola distribution indicates most, if not all of the Holarctic Collembola element in Newfoundland, is naturally Holarctic.

4.3 Effect of Clear-cutting on Collembola Diversity and Abundance

No studies exist on the long term effect of clear-cutting on soil microarthropods of boreal forests with which the present work can be compared directly. There are, however, several studies from North America and Europe on the immediate effect of clear-cutting on Collembola and other microarthropod diversity and abundance (Huhta *et al.* 1967, 1969; Huhta 1976; Vlug and Borden 1973; Seastedt and Crossley 1981; Huhta and Mikkonen 1982 and Bird and Chatarpaul 1986).

Clear-cutting of forests has drastic effects on abiotic soil parameters and on the biota. Removal of forest canopy exposes soil to increased solar radiation which causes higher and more variable soil temperatures during summer and rapid drying of the forest floor after rainfall (Bird and Chatarpaul 1986). Clear-cutting also changes the energy and nutrient input in forest habitats. During and immediately after cutting there are large inputs of cutting wastes, dying roots, and dying soil organisms, however, for several years thereafter the litter-fall inputs are greatly reduced. Collembola communities have shown varied reactions to clear-cutting and forest harvesting. In most cases the density of Collembola decreased soon after clear-cutting (Vlug and Borden 1973; Lasebikan 1975). In some forests a temporary increase in density was observed immediately after clear-cutting (Bird and Chatarpaul 1985), followed by a long-term decline (Huhta 1976). In some cases no change was observed in the faunal composition of Collembola communities (Seastedt and Crossley 1981).

The results of this study showed that clear-cutting did have a long term effect on Collembola communities. In both FD and FE forests the old forest had higher species diversity and abundance than 40 and 60 year old forests. Fewer species, but each generally represented by a greater number of specimens, were collected in FD40 than in FD60 and FDO areas. This resulted in lower diversity indices and evenness values for FD40 sites. In the FD60 forest the diversity of Collembola was greater, but the total abundance was similar to that of FD40 area. This resulted in higher diversity indices and evenness values in the latter area. In the FE forest, the FE40 area had the lowest number of species and specimens but higher diversity index and evenness values than the other aged forests. FE60 and FEO areas were similar in numbers of species and abundance, and diversity and evenness values.

Rarefaction curves for expected number of species in samples from the FD forest also indicated that as forest age increases, so does the diversity of Collembola. However this pattern was complicated by the fact that total abundance of Collembola was low in the FD60 area in all sampling periods. As discussed above under vertical distribution, a fauna of moderate species richness but low specimen density can give relatively high values of H' . This seems to be the case for FD60 areas. Also the faunal conditions in FD60 was different from the other two sites, especially the high density of shrubs and deciduous litter. A shrub, *Kalmia* sp. which produces toxic substance that kills insects, was found in quite large numbers in FD60 sites. Also this site was moister than FD40 and FDO and has lots of large rocks in the ground. These might be the reason for the low numbers of Collembola in FD60 sites.

Although Collembola diversity increased with forest age, some of the species were restricted to or were most abundant in younger forest. Isotomidae was the dominant family in both cut and uncut forests in both forest types during all sampling periods. Vlug and Borden (1973) found that the family Isotomidae became dominant after a forest had been logged and burned. In the present study, *Stenogasterura hiemalis* and *Tomocerus flavescens* were collected only in the old forest of both habitats whereas *Tomocerus minor* and *Willowsia huski* were restricted to regrowth forests. Huhta and Mikkonen (1982) reported that *Tomocerus flavescens* populations were reduced in harvested forests, and Bird and Chatarpaul (1986) found that this species was more abundant on cut forest than on whole-tree harvested forest. This differs from the present study, in which *Tomocerus flavescens* was never present in the cut forests but was replaced there by *Tomocerus minor*.

Bird and Chatarpaul (1986) also found that *Metisotoma grandiceps* and *Lepidocyrtus* spp were more abundant in cut forest than in uncut forest and *Orchesella* spp was more numerous on whole-tree harvested sites than in uncut forest. Similarly, in the present study, *Lepidocyrtus cyaneus* and *Orchesella cincta* were most abundant in cut forest. However, the abundance of *Metisotoma grandiceps* was higher in uncut forest than in cut forest. The dominant species before and after logging and burning in a British Columbia forest (Vlug and Borden 1973), were entirely different from those of the present study. The reason for this difference might be the differing climatic and pedological conditions found in the two provinces and basically different collembolan faunas.

Factor analysis and Discriminant Function analysis showed that as the forest gets older the collembolan community also changes. Both analysis separated FDO from FD40 and FD60 forests indicating that the FDO area has a different diversity and abundance of Collembola species than FD40 and FD60 forests. Principal Component analysis of FE forests separated FEO from FE40 and FE60, but the Discriminant Function analysis separated FE60 from the other two forests, indicating that there is considerable similarity among these ages of forests in Collembola faunas.

The cluster analysis of numerical data showed habitat similarity between FD60 and FDO areas. However the cluster analysis for the presence-absence data grouped FD40 and FD60 areas together. These results indicate that the FD60 area shares faunal similarities with both FD40 and FDO areas, perhaps showing recovery from forest harvesting. Both cluster analyses separated FD forests from FE forests, showing that the FE forest had a different species composition and abundance than FD forests. The TWINSPLAN analysis grouped FD40 and FD60 areas together and grouped FE forest with FDO areas. This showed that area FDO shares some faunal similarities with the FE forest. Seasonal variation in the community of Collembola of FD40 and FD60 areas was also observed. Certain Collembola species were more abundant in early summer and in late summer in FD40 and FD60.

Principal Components ordination of the 3 different aged FD forests based on vegetation, and soil characteristics and the abundance of Collembola grouped FD40 and FD60 sites together and separated FDO sites from them, indicating that the old forest is different

from the other two cut forests in both habitat characteristics and in diversity and distribution of Collembola species. The harvested forests, FD40 and FD60 sites, are generally similar in these 3 sets of characteristics.

The hypothesis that maximum diversity of fauna is maintained in old-growth stands, has been supported by studies on several types of forests (Magcock and Curtis 1960; Auclair and Goff 1971; Connell 1978; Chandler and Peck 1992). Old forests may have a greater diversity of species because the increased leaf litter and old fallen trees on the forest floor provide microhabitats and food resources that do not occur in a young forest where the trees are all the same age (Chandler and Peck 1992). However, a few studies have found higher diversity in forests which have been cut or disturbed in some way. McLeod (1980) suggested that if systems were not disturbed on a moderate scale, the communities therein would be reduced to a low diversity equilibrium through processes of competitive exclusion. That is, soon after a disturbance in a community, many species can co-exist, but after a few years, certain species become established while others die off due to increased competition. Some studies have supported this hypothesis on forest insect communities (Lenksi 1982), but there are no supporting studies for soil microarthropods.

Immediately after clear-cutting, a temporary increase in the number of microarthropods has been reported. However, numbers may then decrease and stay low for a long time thereafter (Vlug and Borden 1973). This has been attributed to increased amounts of available food after clear-cutting, which gradually became depleted from the clear-cut areas

(Huhta *et al.* 1967). Although soil temperature, moisture, and nutrient conditions of a harvested forest may approach precutting conditions within four years (Covington 1981), the faunal densities in harvested forests may take longer than this to return to original conditions (Bird and Chatarpaul 1986). Reduced faunal (beetles) densities have been observed 9 to 10 years after clear cutting (Niemela *et al.* 1993), and reduced bacterial and enchytraeids densities were observed 10 to 13 years after clear-cutting (Sundman *et al.* 1978). Vlug and Borden (1973) reported (after Karppinen 1957) that 27 years after burning, the microarthropod fauna was still different from the original, even though the total density had largely returned to the original level.

The present study demonstrates that clear-cutting does have a long term effect on the diversity and abundance of Collembola. After clear-cutting and 40 years of regeneration, the diversity and abundance of Collembola were less than that of uncut forest. The 40 year old forest had a lower density and diversity of Collembola than the old forest. With increasing forest age species diversity recovered, but some Collembola species disappeared, whereas others appeared and total abundance and dominance patterns changed. The 60-year-old forest shared some faunal similarities with both 40-year-old and old forests, indicating that even after 60 years recovery is still in progress. The old forest contains two Collembola species, *Tomocerus flavescens* and *Stenogasterura hiemalis*, that are absent from harvested forests. Previous studies have shown that Collembola are important soil insects and show a stable community structure with large numbers and high diversity and serve as useful indicators of forest conditions. This has been supported by my study which further indicates that

Collembola have good potential for use in forest classification and for analysis of the impact of various natural and human disturbances in boreal forests. If forest harvesting is carried out on a cyclical basis, that is every 50 to 60 years, this might result in permanent change to Collembola communities and consequently in productivity of Newfoundland balsam fir forests.

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6. APPENDICES

Appendix A. Mean densities (1000/cm³) of Collembola species collected from each site from each sampling date.

FDO-1, 1992

SPECIES	JULY		AUGUST	
	MEAN	ST. DEV	MEAN	ST. DEV
<i>Hypogastrura loricata</i>	1.6	2.3	1.9	1.8
<i>Hypogastrura humi</i>	23.6	33.4	13.9	11.6
<i>Willemia denisi</i>	0.1	0.5	0.0	0.0
<i>Willemia intermedia</i>	1.2	1.5	0.8	1.2
<i>Friesca submilis</i>	0.4	0.8	0.2	0.4
<i>Pseudachorutes suberassoides</i>	2.2	5.9	2.3	1.7
<i>Pseudachorutes aureofasciatus</i>	0.1	0.2	0.0	0.0
<i>Anurida pygmaea</i>	0.5	0.8	0.1	0.3
<i>Anurida furcifera</i>	0.1	0.2	0.0	0.0
<i>Neamira muscorum</i>	0.3	0.7	0.2	0.4
<i>Onychiurus similis</i>	1.6	2.0	0.1	0.7
<i>Onychiurus paro</i>	9.6	9.7	21.0	14.2
<i>Onychiurus affinis</i>	6.6	7.7	3.7	4.3
<i>Tullbergia granulata</i>	19.0	55.0	13.4	9.4
<i>Anuraphorus binoculatus</i>	0.7	0.5	0.3	0.5
<i>Folsomia penicula</i>	181.1	130.3	168.8	130.0
<i>Metisotoma grandiceps</i>	7.1	5.9	5.0	4.8
<i>Micrisotoma achromata</i>	4.9	4.1	2.9	3.4
<i>Isotomiella minor</i>	39.6	47.3	69.2	51.2
<i>Isotomurus sp</i>	1.7	1.9	0.0	0.0
<i>Isotoma notabilis</i>	4.0	5.3	1.7	2.3
<i>Isotoma trispinata</i>	5.6	5.0	6.0	5.6
<i>Isotoma manitobae</i>	12.8	5.7	8.3	5.7
<i>Isotoma hiemalis</i>	5.3	2.7	2.1	2.1
<i>Isotoma sp 3</i>	1.6	2.1	0.2	0.4
<i>Isotoma sp 4</i>	1.9	5.1	1.4	3.1
<i>Isotoma sp 5</i>	0.3	0.6	0.0	0.0
<i>Isotoma viridis</i>	0.5	1.0	7.1	6.3
<i>Entomobrya multifasciata</i>	0.0	0.0	0.5	0.7
<i>Tomocerus flavescens</i>	1.7	2.0	0.4	0.5
<i>Sminthurides lepus</i>	0.7	2.1	0.0	0.0
<i>Arrhopalites benitus</i>	0.0	0.0	0.2	0.4
<i>Arrhopalites hirtus</i>	0.2	0.7	0.1	0.3
<i>Arrhopalites diversus</i>	1.0	1.9	1.4	2.0
<i>Sminthurinus quadrimaculatus</i>	0.0	0.0	0.4	0.7
<i>Sminthurinus henshawi</i>	0.2	0.5	0.0	0.0
<i>Sminthurus sp 1</i>	0.0	0.0	0.2	0.4
<i>Sminthurus sp 2</i>	0.0	0.0	0.1	0.3
Total mean density	337.7		333.9	
Total # species	33		31	

SPECIES	JUNE		JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	10.0	11.2	2.1	2.4	6.7	7.4
<i>Hypogastrura humi</i>	5.1	3.5	4.6	3.1	0.0	0.0
<i>Stenogastrura hiemalis</i>	0.7	1.0	0.8	1.3	2.1	2.3
<i>Willemia denisi</i>	9.6	8.9	0.4	0.8	0.0	0.0
<i>Willemia intermedia</i>	13.7	9.5	6.6	6.1	1.7	2.3
<i>Friesea submillis</i>	0.9	1.3	0.6	0.5	0.6	0.7
<i>Pseudachorutes subcrassoides</i>	5.1	5.2	3.6	3.4	5.4	3.8
<i>Pseudachorutes aureofasciatus</i>	0.3	0.7	0.2	0.6	0.0	0.0
<i>Anurida pygmaea</i>	2.7	2.0	3.3	2.7	2.2	3.3
<i>Anurida furcifera</i>	1.1	1.2	0.3	1.0	0.4	0.7
<i>Neanura muscorum</i>	0.8	1.9	0.7	1.1	0.6	0.7
<i>Onychiurus similis</i>	6.2	11.4	13.4	15.7	17.3	11.1
<i>Onychiurus paro</i>	15.8	14.7	15.0	10.8	14.1	6.7
<i>Onychiurus affinis</i>	7.3	9.2	3.3	6.7	11.3	11.0
<i>Tullbergia granulata</i>	5.5	8.6	3.8	3.9	6.1	6.5
<i>Anurophorus binoculatus</i>	2.3	2.0	0.7	1.3	1.0	0.8
<i>Folsomia penicula</i>	471.7	238.6	522.6	405.2	422.0	193.8
<i>Metisotoma grandiceps</i>	10.4	5.2	10.9	9.2	14.4	10.4
<i>Micrisotoma achromata</i>	2.0	1.5	0.9	0.7	1.5	1.1
<i>Isotomiella minor</i>	50.1	22.6	52.3	18.9	48.1	29.1
<i>Isotomurus sp</i>	21.0	13.2	8.7	15.0	3.8	5.2
<i>Isotoma «kmari</i>	0.2	0.4	0.0	0.0	0.0	0.0
<i>Isotoma notabilis</i>	22.3	14.4	17.5	9.9	20.3	11.8
<i>Isotoma trispinata</i>	11.4	7.1	15.8	9.3	17.2	14.3
<i>Isotoma manitobae</i>	10.8	10.3	4.9	3.8	5.2	5.9
<i>Isotoma hiemalis</i>	0.1	0.3	1.6	5.1	0.2	0.4
<i>Isotoma sp 3</i>	0.3	0.1	0.2	0.4	0.3	0.7
<i>Isotoma viridis</i>	0.1	0.3	1.8	3.0	1.2	1.5
<i>Entomobrya multifasciata</i>	0.1	0.3	1.4	2.2	1.6	2.1
<i>Lepidocyrtus cyaneus</i>	0.3	0.3	0.0	0.0	0.1	0.3
<i>Tomocerus sp</i>	1.1	2.2	5.2	4.2	2.0	2.3
<i>Nechus minimus</i>	1.0	0.9	0.1	0.3	6.1	6.5
<i>Sminthurides lepus</i>	1.6	1.7	0.0	0.0	0.7	0.7
<i>Arrhopalites benitus</i>	2.7	2.0	1.0	2.0	0.0	0.0
<i>Arrhopalites hirtus</i>	1.7	1.8	0.7	1.0	4.0	4.6
<i>Arrhopalites diversus</i>	0.3	0.5	0.0	0.0	0.1	0.3
<i>Sminthurinus quadrimaculatus</i>	1.4	1.8	0.2	0.4	0.0	0.0
<i>Sminthurinus henschawi</i>	0.4	0.7	0.3	0.7	0.0	0.0
<i>Sminthurus sp 1</i>	0.3	1.0	0.0	0.0	0.0	0.0
<i>Sminthurus sp 2</i>	0.1	0.3	0.1	0.3	0.5	0.9
Total mean density	699.2		705.6		618.6	
Total # species	39		35		31	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	2.2	1.6	3.1	2.9
<i>Hypogastrura humi</i>	6.7	16.0	9.6	8.1
<i>Willemia dentisi</i>	0.2	0.5	0.0	0.0
<i>Willemia intermedia</i>	1.1	1.6	2.2	2.6
<i>Friesca submilis</i>	0.2	0.9	0.0	0.0
<i>Pseudachorutes subcrassoides</i>	1.3	1.3	1.1	1.5
<i>Anurid - ygamea</i>	1.0	1.2	1.1	2.1
<i>Anurida furcifera</i>	0.0	0.0	0.1	0.3
<i>Neanura muscorum</i>	0.2	0.9	0.7	1.6
<i>Onychiurus similis</i>	0.4	1.8	0.0	0.0
<i>Onychiurus paro</i>	12.9	9.6	10.9	8.2
<i>Onychiurus affinis</i>	6.6	6.3	4.2	3.1
<i>Tullbergia granulata</i>	4.5	4.1	8.5	10.8
<i>Anuraphorus binocularis</i>	0.0	0.0	0.1	0.3
<i>Folsomia penicula</i>	185.0	140.1	192.1	135.4
<i>Metisotoma grandiceps</i>	4.1	3.1	6.1	5.6
<i>Micrisotoma achromata</i>	4.6	6.5	2.7	3.7
<i>Isotomiella minor</i>	37.8	57.0	121.0	78.9
<i>Isotomurus sp</i>	1.0	1.9	0.5	1.6
<i>Isotoma notabilis</i>	4.6	3.9	3.4	2.1
<i>Isotoma trispinata</i>	4.4	6.0	5.5	3.1
<i>Isotoma manitobae</i>	7.1	7.6	4.1	3.3
<i>Isotoma hiemalis</i>	3.6	2.3	2.3	2.2
<i>Isotoma sp 3</i>	0.7	1.3	0.1	0.3
<i>Isotoma sp 4</i>	0.1	0.5	0.2	0.6
<i>Isotoma sp 5</i>	0.8	1.6	0.3	0.5
<i>Isotoma beta</i>	0.1	0.2	0.0	0.0
<i>Isotoma viridis</i>	1.5	1.4	2.5	2.7
<i>Entomobrya multifasciata</i>	0.3	0.5	0.5	0.9
<i>Tomocerius flavescens</i>	0.5	0.5	0.7	0.5
<i>Tomocerius Sp</i>	0.0	0.0	0.1	0.3
<i>Sminthurides lepus</i>	0.2	0.7	0.0	0.0
<i>Arrhopalites benitus</i>	0.4	0.8	0.0	0.0
<i>Arrhopalites hirtus</i>	0.1	0.3	0.0	0.0
<i>Arrhopalites diversus</i>	1.7	2.6	0.4	0.7
<i>Sminthurinus quadrimaculatus</i>	0.0	0.0	0.6	1.1
<i>Sminthurinus henshawi</i>	0.1	0.5	0.0	0.0
<i>Sminthurus sp 1</i>	0.2	0.6	0.0	0.0
Total mean density	298.8		384.7	
Total # species	34		25	

SPECIES	JUNE		JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	8.8	15.5	5.4	5.1	1.5	2.8
<i>Hypogastrura humi</i>	11.0	6.8	15.4	32.1	5.9	6.6
<i>Senogastrura hiemalis</i>	0.2	0.4	0.1	0.3	0.1	0.3
<i>Willemia denisi</i>	0.8	1.7	0.0	0.0	0.1	0.3
<i>Willemia intermedia</i>	10.6	8.7	12.4	8.6	5.4	10.5
<i>Friesea subnilis</i>	1.5	1.6	0.2	0.4	3.0	9.1
<i>Pseudachorutes suberassoides</i>	7.4	8.2	2.9	2.9	11.4	10.0
<i>Pseudachorutes aureofasciatus</i>	0.7	2.2	0.0	0.0	0.6	1.9
<i>Anurida pygmaea</i>	2.0	1.4	1.7	1.8	4.2	5.7
<i>Anurida furcifera</i>	1.5	2.1	0.9	1.1	1.1	1.6
<i>Onychiurus similis</i>	7.7	19.5	2.1	3.2	1.4	2.5
<i>Onychiurus paro</i>	38.6	22.4	10.3	6.6	24.6	24.1
<i>Onychiurus affinis</i>	60.3	60.3	13.9	15.0	18.8	40.8
<i>Tullbergia granulata</i>	18.9	17.1	13.1	12.4	3.8	4.7
<i>Neanura muscorum</i>	5.5	6.7	0.6	0.7	4.8	8.4
<i>Anurophorus binoculatus</i>	2.2	1.7	2.0	1.5	1.0	1.6
<i>Folsomia penicula</i>	576.4	222.5	324.6	160.2	460.8	197.2
<i>Metisotoma grandiceps</i>	5.4	4.5	5.1	3.8	8.3	6.6
<i>Micrisotoma achromata</i>	1.5	1.5	1.2	0.6	0.8	0.9
<i>Isotomiella minor</i>	71.9	44.1	79.0	15.0	56.5	15.1
<i>Isotomurus sp</i>	11.1	15.7	6.8	7.7	27.0	47.6
<i>Isotoma notabilis</i>	20.6	13.6	21.5	16.5	9.4	9.5
<i>Isotoma trispinata</i>	17.8	13.6	5.0	5.5	13.3	7.2
<i>Isotoma wanitobae</i>	2.9	3.3	5.9	6.9	1.8	1.8
<i>Isotoma hiemalis</i>	1.2	2.3	0.8	2.5	1.5	3.2
<i>Isotoma sp 3</i>	0.4	1.0	0.2	0.4	0.5	0.7
<i>Isotoma viridis</i>	0.8	0.6	0.3	0.5	3.2	2.3
<i>Eutomobrye multifasciata</i>	0.0	0.0	3.3	4.0	0.9	1.6
<i>Lepidocyrtus cyaneus</i>	0.0	0.0	0.3	0.4	0.1	0.1
<i>Tomocerus sp</i>	0.5	0.7	5.5	6.4	4.6	3.0
<i>Neelus minimus</i>	0.6	0.8	0.1	0.3	1.0	1.5
<i>Sminthurides lepus</i>	1.0	1.7	0.0	0.0	1.9	1.6
<i>Arrhopalites benitus</i>	0.3	0.7	0.1	0.3	0.0	0.0
<i>Arrhopalites hirtus</i>	1.9	2.6	1.4	1.9	0.4	0.5
<i>Arrhopalites diversus</i>	1.0	1.5	0.0	0.0	0.0	0.0
<i>Sminthurinus quadrimaculatus</i>	0.2	0.4	0.6	1.3	0.0	0.0
<i>Sminthurinus henshawi</i>	0.0	0.0	1.6	4.4	0.6	1.5
<i>Sminthurus sp 1</i>	0.3	0.5	0.0	0.0	0.0	0.0
<i>Sminthurus sp 2</i>	0.1	0.3	0.0	0.0	0.1	0.3
Total mean density	893.6		544.0		680.3	
Total # species	36		32		34	

SPECIES	FDO-1		FDO-2	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	3.7	4.5	2.7	2.5
<i>Hypogastrura huxi</i>	21.5	28.3	5.3	3.4
<i>Stenogastrura hiemalis</i>	1.0	1.5	0.2	0.4
<i>Willemia denisi</i>	0.0	0.0	0.3	0.5
<i>Willemia intermedia</i>	4.7	4.2	7.1	9.5
<i>Friessea submitis</i>	0.3	0.7	2.7	7.5
<i>Friessea alaskella</i>	1.2	1.4	0.6	1.9
<i>Pseudachorutes auberassoides</i>	6.0	6.4	9.1	7.8
<i>Pseudachorutes aureofasciatus</i>	0.6	0.8	1.0	1.6
<i>Anurida pygmaea</i>	3.3	3.1	1.7	2.0
<i>Anurida furcifera</i>	1.6	1.6	0.8	0.8
<i>Neanura muscorum</i>	1.2	1.7	2.3	2.8
<i>Onychiurus similis</i>	29.9	42.0	11.8	11.0
<i>Onychiurus poro</i>	20.3	23.1	14.0	7.2
<i>Onychiurus affinis</i>	4.4	7.1	0.7	1.0
<i>Tullbergia granulata</i>	3.9	4.5	9.8	8.5
<i>Anurophorus binoculatus</i>	5.6	5.1	5.4	4.2
<i>Folsomia penicula</i>	386.3	175.4	517.4	201.1
<i>Metisotomo grandiceps</i>	12.0	6.3	6.7	6.8
<i>Micrisotoma acchromata</i>	7.5	5.7	4.1	4.9
<i>Isotomiella minor</i>	93.1	102.7	111.8	75.3
<i>Isotomurus sp</i>	57.4	42.7	38.9	41.9
<i>Isotoma notabilis</i>	116.5	94.5	48.8	46.1
<i>Isotoma manitobae</i>	3.5	5.8	2.1	2.0
<i>Isotoma hiemalis</i>	3.4	3.9	3.2	3.2
<i>Isotoma sp 1</i>	6.1	6.8	3.8	5.6
<i>Isotoma sp 2</i>	0.6	1.1	0.5	0.7
<i>Isotoma sp 3</i>	1.3	1.2	0.5	0.7
<i>Isotoma viridis</i>	0.6	0.8	0.5	0.7
<i>Entomobrya multifasciata</i>	0.1	0.3	0.0	0.0
<i>Tomoceris flavescens</i>	0.5	0.9	0.3	0.7
<i>Tomoceris sp</i>	18.0	10.5	6.2	7.6
<i>Necurus minimus</i>	10.8	8.5	12.7	13.3
<i>Sminthurides lepus</i>	7.5	6.2	6.4	10.5
<i>Arrhopalites benitus</i>	5.5	3.9	3.9	5.2
<i>Arrhopalites hirtus</i>	4.8	9.8	0.3	0.5
<i>Arrhopalites diversus</i>	1.0	0.7	2.5	1.7
<i>Sminthurinus quadrimaculatus</i>	0.0	0.0	0.3	0.5
<i>Sminthurinus henshawi</i>	0.9	1.7	0.4	1.3
<i>Sminthurus sp 1</i>	0.6	1.1	0.4	1.0
<i>Sminthurus sp 2</i>	1.9	2.6	0.1	0.3
unidentified	0.5	1.3	0.0	0.0
Total mean density	850.1		847.4	
Total # species	41		41	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	1.6	3.8	4.6	5.4
<i>Hypogastrura humi</i>	1.3	1.5	19.5	29.5
<i>Willemia denisi</i>	0.2	0.7	0.0	0.0
<i>Willemia intermedia</i>	1.1	2.1	3.8	7.2
<i>Friesea submillis</i>	1.0	1.3	3.7	9.3
<i>Pseudachorutes subcrassoides</i>	0.0	0.0	4.6	7.0
<i>Anurida pygmaea</i>	1.3	1.8	0.9	1.9
<i>Anurida furcifera</i>	0.4	0.9	0.0	0.0
<i>Neanura muscorum</i>	0.1	0.2	1.2	2.1
<i>Onychiurus similis</i>	2.2	4.1	9.1	9.2
<i>Onychiurus paro</i>	8.5	6.1	21.9	16.8
<i>Onychiurus affinis</i>	0.5	1.3	4.7	6.7
<i>Tullbergia granulata</i>	5.3	5.4	9.8	6.5
<i>Anurophorus binoculatus</i>	0.0	0.0	0.1	0.3
<i>Folsomia penicula</i>	52.2	27.1	63.5	26.6
<i>Meisotoma grandiceps</i>	0.8	1.1	5.0	9.2
<i>Micrisotoma achromata</i>	0.2	0.5	0.9	1.5
<i>Isotomiella minor</i>	92.6	155.5	171.7	199.6
<i>Isotoma notabilis</i>	6.6	6.1	11.7	11.1
<i>Isotoma trispinata</i>	5.8	6.8	7.7	6.8
<i>Isotoma manitobae</i>	0.1	0.2	1.4	1.9
<i>Isotoma viridis</i>	5.9	5.0	4.5	6.3
<i>Entomobrya multifasciata</i>	1.5	3.8	1.8	3.6
<i>Willowsia buski</i>	0.5	1.0	0.6	1.3
<i>Tomocerus minor</i>	0.2	0.6	0.0	0.0
<i>Neelus minimus</i>	0.1	0.2	0.0	0.0
<i>Arrhopalites diversus</i>	0.2	0.5	0.6	0.1
Total mean density	190.2		353.3	
Total # species	25		23	

SPECIES	JUNE		JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	7.6	17.1	3.5	3.4	4.5	4.2
<i>Hypogastrura humi</i>	6.1	11.1	1.1	3.5	0.0	0.0
<i>Willemia denisi</i>	6.7	6.7	0.3	0.7	1.2	2.9
<i>Willemia intermedia</i>	20.4	15.1	10.0	15.0	5.7	6.7
<i>Friesea submilis</i>	7.5	10.9	0.8	0.9	4.4	3.4
<i>Pseudachorutes subcrassoides</i>	0.8	1.3	1.0	1.3	1.2	1.1
<i>Pseudachorutes aureofasciatus</i>	0.0	0.0	0.8	1.0	0.0	0.0
<i>Anurida pygmaea</i>	2.2	3.5	3.2	2.7	1.4	1.1
<i>Anurida fureifera</i>	4.8	7.4	0.9	1.0	2.4	1.7
<i>Neanura muscorum</i>	1.8	3.7	0.1	0.3	4.7	3.0
<i>Onychiurus similis</i>	7.0	10.3	5.8	6.0	9.4	2.9
<i>Onychiurus paro</i>	44.4	33.6	31.7	35.4	22.7	8.5
<i>Onychiurus affinis</i>	6.4	9.3	19.0	15.1	12.8	9.2
<i>Tullbergia granulata</i>	14.1	12.1	18.6	23.1	11.9	7.5
<i>Anurophorus binoculatus</i>	1.5	1.7	2.0	2.8	0.9	1.5
<i>Folsomia penicula</i>	354.7	248.1	198.2	111.1	232.3	136.7
<i>Metisotoma grandiceps</i>	1.1	1.1	1.5	1.5	1.6	2.6
<i>Micrisotoma achromata</i>	1.1	2.3	0.3	0.7	0.9	1.1
<i>Isotomiella minor</i>	37.3	59.0	42.3	51.0	71.9	50.9
<i>Isotomurus</i> sp	0.1	0.3	0.0	0.0	0.0	0.0
<i>Isotoma notabilis</i>	15.4	13.4	13.9	13.1	11.4	7.8
<i>Isotoma trispinata</i>	15.6	12.0	9.0	6.7	20.8	10.2
<i>Isotoma hiemalis</i>	0.0	0.0	0.0	0.0	0.9	2.9
<i>Isotoma</i> sp 5	0.0	0.0	0.3	0.1	0.0	0.0
<i>Isotoma viridis</i>	0.3	0.7	0.0	0.0	0.0	0.0
<i>Ochesella cincta</i>	0.1	0.3	1.6	1.8	2.9	3.2
<i>Entomobrya multifasciata</i>	0.0	0.0	2.2	4.2	2.7	2.3
<i>Willowisia buski</i>	0.0	0.0	0.1	0.3	0.1	0.3
<i>Necelus minimus</i>	1.1	8.8	0.8	1.1	2.3	2.2
<i>Sminthurides lepus</i>	0.0	0.0	0.3	0.5	1.0	1.6
<i>Arrhopalites hirtus</i>	4.7	4.7	0.0	0.0	1.3	1.5
<i>Sminthurus</i> sp 1	0.4	0.7	0.0	0.0	0.0	0.0
<i>Sminthurus</i> sp 2	0.0	0.0	0.1	0.3	0.0	0.0
Total mean density	547.6		368.5		433.3	
Total # species	26		28		26	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	2.7	3.2	3.7	4.3
<i>Hypogastrura humi</i>	8.2	9.0	17.3	16.9
<i>Willemia intermedia</i>	2.6	3.0	2.1	2.0
<i>Friesea submillis</i>	1.0	1.4	1.2	1.2
<i>Pseudachorutes suberassoides</i>	0.4	0.7	0.8	1.3
<i>Anurida pygmaea</i>	1.3	1.3	1.3	1.0
<i>Anurida furcifera</i>	1.1	1.6	1.1	1.1
<i>Neanura muscorum</i>	0.0	0.0	1.5	1.5
<i>Onychiurus similis</i>	4.7	6.1	8.4	9.6
<i>Onychiurus paro</i>	10.9	8.0	20.7	26.5
<i>Onychiurus affinis</i>	2.9	4.9	3.1	5.7
<i>Tullbergia granulata</i>	3.7	5.7	10.3	11.0
<i>Folsomia penicula</i>	79.1	32.3	84.5	39.8
<i>Metisotoma grandiceps</i>	1.4	1.2	1.2	1.4
<i>Micrisotoma achromata</i>	1.1	1.4	2.6	3.8
<i>Isotomiella minor</i>	96.4	134.6	141.0	156.7
<i>Isotoma notabilis</i>	10.4	12.2	6.9	6.8
<i>Isotoma trispinata</i>	13.1	15.3	4.0	6.9
<i>Isotoma viridis</i>	6.9	6.0	3.2	3.3
<i>Entomobrya multifasciata</i>	1.8	2.3	0.7	1.1
<i>Willowsia buski</i>	0.5	0.8	0.4	1.0
<i>Neehus minimus</i>	0.1	0.2	0.1	0.3
<i>Arrhopalites diversus</i>	0.2	0.4	0.0	0.0
<i>Sminthurinus quadrimaculatus</i>	0.0	0.0	0.2	0.4
Total mean density	250.5		316.3	
Total # species	22		23	

SPECIES	JUNE		JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	5.1	11.8	1.0	1.1	17.8	25.9
<i>Willemia denisi</i>	3.7	7.2	0.0	0.0	0.0	0.0
<i>Willemia intermedia</i>	30.7	10.4	6.9	7.0	28.2	23.9
<i>Friesea submilis</i>	2.5	4.6	0.3	0.7	0.0	0.0
<i>Pseudachorutes suberassoides</i>	1.1	1.1	0.8	1.3	4.1	3.3
<i>Pseudachorutes aureofasciatus</i>	0.0	0.0	0.6	1.3	0.3	0.5
<i>Amurida pygmaea</i>	0.8	0.9	3.2	4.2	2.6	4.3
<i>Amurida furcifera</i>	2.7	1.6	0.6	1.4	0.2	0.4
<i>Neanura muscorum</i>	0.3	0.5	0.2	0.6	1.8	2.3
<i>Onychiurus similis</i>	6.8	9.3	2.4	2.3	2.9	4.9
<i>Onychiurus paro</i>	34.5	45.6	14.7	12.0	7.2	8.3
<i>Onychiurus affinis</i>	11.6	20.2	14.8	14.8	24.1	17.1
<i>Tullbergia granulata</i>	24.1	26.3	10.2	9.1	9.1	10.4
<i>Anurophorus binoculatus</i>	0.3	0.7	2.7	2.4	0.7	0.9
<i>Folsomia penicula</i>	489.1	335.6	344.6	290.3	375.9	221.3
<i>Metisotoma grandiceps</i>	1.1	1.5	1.8	2.8	2.7	2.7
<i>Micrisotoma achromata</i>	0.5	1.6	7.5	8.8	1.4	2.8
<i>Isotomiella minor</i>	75.4	90.7	123.5	143.8	68.8	83.3
<i>Isotomurus sp</i>	0.0	0.0	0.4	0.8	1.0	1.5
<i>Isotoma notabilis</i>	7.6	8.6	17.9	24.9	24.1	32.5
<i>Isotoma trispinata</i>	7.2	6.9	8.5	11.5	11.7	11.2
<i>Isotoma hiemalis</i>	0.1	0.3	0.0	0.0	0.3	0.7
<i>Isotoma sp 4</i>	0.0	0.0	0.2	0.4	0.1	0.3
<i>Isotoma viridis</i>	1.1	1.0	0.1	0.3	0.0	0.0
<i>Orchesella cincta</i>	0.0	0.0	0.8	0.8	1.8	1.8
<i>Entomobrya multifasciata</i>	0.0	0.0	3.1	5.5	1.2	2.0
<i>Tomocerus minor</i>	0.0	0.0	0.0	0.0	0.3	0.7
<i>Tomocerus sp</i>	0.0	0.0	0.1	0.3	0.0	0.0
<i>Necelus minimus</i>	0.8	0.9	2.4	3.4	2.3	3.0
<i>Smynthurides lepus</i>	0.0	0.0	0.1	0.3	1.3	1.3
<i>Arrhopalites benitus</i>	0.0	0.0	0.0	0.0	0.4	0.7
<i>Arrhopalites hirtus</i>	2.7	4.3	0.0	0.0	0.1	0.3
<i>Smynthurinus quadrimaculatus</i>	0.0	0.0	0.1	0.3	0.2	0.6
Total mean density	709.8		552.9		592.4	
Total # species	23		28		28	

SPECIES	FD40-3		FD40-4	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	9.1	12.9	1.9	2.5
<i>Hypogastrura humi</i>	0.4	0.7	0.0	0.0
<i>Willemia denisi</i>	0.5	0.9	0.6	1.4
<i>Willemia intermedia</i>	8.0	7.3	17.0	22.3
<i>Friesea submillis</i>	0.0	0.0	0.7	1.9
<i>Friesea alaskella</i>	0.2	0.7	0.0	0.0
<i>Pseudachorutes subcrassoides</i>	3.8	3.6	2.1	2.6
<i>Pseudachorutes aureofasciatus</i>	0.0	0.0	0.8	0.6
<i>Anurida pygmaea</i>	3.3	3.8	4.5	4.7
<i>Anurida furcifera</i>	0.2	0.4	1.6	2.2
<i>Neanura muscorum</i>	0.4	1.3	0.4	0.7
<i>Onychiurus similis</i>	32.4	28.1	40.3	34.4
<i>Onychiurus paro</i>	20.0	18.0	19.2	31.9
<i>Onychiurus affinis</i>	3.7	6.2	7.2	9.2
<i>Tullbergia granulata</i>	15.1	16.5	18.3	21.4
<i>Anurophorus binoculatus</i>	6.3	6.0	15.5	13.1
<i>Folsomia penicula</i>	241.7	127.7	421.3	427.8
<i>Metisotoma grandiceps</i>	2.2	3.7	1.6	1.3
<i>Micrisotoma achromata</i>	2.1	2.5	13.3	9.6
<i>Isotomiella minor</i>	48.7	45.5	111.9	55.7
<i>Isotoma notabilis</i>	42.8	41.0	27.4	24.7
<i>Isotoma trispinata</i>	0.4	1.0	5.7	8.7
<i>Isotoma sp 1</i>	0.9	1.1	1.1	1.4
<i>Isotoma sp 2</i>	0.0	0.0	0.1	0.3
<i>Entomobrya multifasciata</i>	0.0	0.0	0.9	2.5
<i>Tomocerius sp</i>	0.0	0.0	1.1	1.5
<i>Neeus minimus</i>	25.4	26.1	26.6	19.9
<i>Sminthurides lepus</i>	1.9	1.5	2.8	2.8
<i>Arrhopalites benitus</i>	0.0	0.0	0.1	0.3
<i>Arrhopalites diversus</i>	0.3	0.7	0.3	0.7
Total mean density	469.8		744.5	
Total # species	24		29	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	0.1	0.2	0.0	0.0
<i>Hypogastrura humi</i>	2.3	4.2	1.7	2.3
<i>Willemia denisi</i>	0.4	0.8	0.6	0.8
<i>Willemia intermedia</i>	3.2	2.9	2.7	2.2
<i>Friesea submillis</i>	2.8	3.8	2.4	2.6
<i>Pseudachorates aureofasciatus</i>	0.2	0.5	0.0	0.0
<i>Anurida pygmaea</i>	0.5	1.1	2.3	1.6
<i>Anurida furcifera</i>	0.2	0.4	0.5	0.7
<i>Neanura muscorum</i>	0.1	0.3	0.7	1.5
<i>Onychiurus similis</i>	2.2	3.0	3.1	4.0
<i>Onychiurus paro</i>	6.5	6.3	3.2	3.1
<i>Onychiurus affinis</i>	4.0	4.6	2.1	3.5
<i>Tullbergia granulata</i>	6.9	7.4	9.8	9.9
<i>Anuropharus binoculatus</i>	0.4	0.6	0.9	0.8
<i>Folsomia penicula</i>	55.2	39.6	46.1	39.6
<i>Metisotoma grandiceps</i>	0.6	1.1	1.4	1.8
<i>Micrisotoma achromata</i>	0.6	1.1	5.3	6.7
<i>Isotoniella minor</i>	95.2	115.5	40.3	65.1
<i>Isotoma notabilis</i>	4.7	5.0	4.8	3.9
<i>Isotoma trispinata</i>	7.6	9.6	5.2	4.9
<i>Isotoma manitobae</i>	0.0	0.0	0.4	1.3
<i>Isotoma viridis</i>	4.9	6.2	4.2	6.6
<i>Entomobrya multifasciata</i>	1.4	2.7	3.5	5.5
<i>Willowsia huski</i>	0.0	0.0	0.5	0.7
<i>Tomocerius minor</i>	0.7	1.3	0.8	1.0
<i>Tomocerius</i> sp	0.1	0.2	3.5	5.5
<i>Arrhopalites diversus</i>	0.0	0.0	0.1	0.3
Total mean density	200.8		143.0	
Total # species	24		25	

SPECIES	JUNE		JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	0.2	0.6	1.0	1.3	1.0	2.0
<i>Hypogastrura humi</i>	0.1	0.3	0.0	0.0	0.0	0.0
<i>Willemia denisi</i>	1.0	1.9	1.3	2.1	2.1	3.8
<i>Willemia intermedia</i>	2.1	2.5	1.3	1.7	6.0	4.9
<i>Friesea submilis</i>	1.2	1.8	2.3	3.2	3.5	4.6
<i>Pseudachorutes subcrassoides</i>	0.1	0.3	0.2	0.6	1.2	1.7
<i>Anurida pygmaea</i>	0.4	0.5	0.1	0.3	0.8	0.9
<i>Anurida furcifera</i>	2.2	3.1	1.0	1.6	0.1	0.3
<i>Neanura muscorum</i>	0.7	1.3	1.3	1.3	0.8	0.9
<i>Onychiurus similis</i>	8.4	7.7	11.4	9.1	7.6	13.5
<i>Onychiurus paro</i>	3.5	2.8	4.2	3.2	4.3	3.2
<i>Onychiurus affinis</i>	9.5	11.6	1.3	1.9	14.1	9.8
<i>Tullbergia granulata</i>	25.2	17.6	27.8	30.7	11.7	6.6
<i>Anurophorus binoculatus</i>	0.8	1.3	0.2	0.4	0.5	1.1
<i>Folsomia penicula</i>	117.1	134.9	99.7	139.8	136.6	103.6
<i>Meisotoma grandiceps</i>	0.6	1.0	0.7	0.8	1.5	1.5
<i>Micrisotoma achromata</i>	12.1	15.5	3.1	3.6	2.6	6.5
<i>Isotomiella minor</i>	94.1	62.0	76.3	46.3	53.5	50.2
<i>Isotomurus sp</i>	0.0	0.0	1.0	2.8	7.5	11.3
<i>Isotoma notabilis</i>	5.3	4.6	12.3	30.9	19.4	27.9
<i>Isotoma trispinata</i>	1.0	1.2	32.0	42.2	8.4	8.7
<i>Isotoma manitobae</i>	0.0	0.0	0.0	0.0	0.2	0.4
<i>Isotoma sp 5</i>	1.3	1.7	0.0	0.0	0.0	0.0
<i>Isotoma viridis</i>	0.6	0.8	1.3	2.5	0.5	0.7
<i>Orchesella cincta</i>	0.5	0.7	5.4	7.9	0.9	1.1
<i>Entomobrya multifasciata</i>	0.0	0.0	3.9	4.6	3.3	5.0
<i>Willowsia buski</i>	0.0	0.0	0.0	0.0	0.2	0.6
<i>Tomocerus minor</i>	0.0	0.0	0.0	0.0	0.3	0.7
<i>Neeelus minimus</i>	0.0	0.0	0.8	1.0	0.5	1.3
<i>Sminthurides lepus</i>	0.1	0.3	0.1	0.3	0.0	0.0
<i>Arrhopalites benitus</i>	0.1	0.3	0.1	0.3	0.0	0.0
<i>Arrhopalites diversus</i>	0.1	0.3	0.0	0.0	0.0	0.0
<i>Sminthurus sp 1</i>	0.1	0.3	0.0	0.0	0.0	0.0
<i>Sminthurus sp 2</i>	0.1	0.3	0.0	0.0	0.0	0.0
<i>Dicyrtoma fusca</i>	0.0	0.0	0.0	0.0	0.3	0.7
Total mean density	289.7		290.2		297.2	
Total # species	28		26		28	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	0.0	0.0	0.3	1.0
<i>Hypogastrura humi</i>	12.3	9.9	4.3	9.1
<i>Willemia intermedia</i>	0.4	0.9	0.6	1.4
<i>Friessea submilis</i>	1.3	2.4	1.1	1.5
<i>Pseudachorutes subcrassoides</i>	0.1	0.2	1.2	3.1
<i>Anurida pygmaea</i>	0.7	1.1	1.0	1.3
<i>Anurida furcifera</i>	0.0	0.0	0.1	0.3
<i>Neanura muscorum</i>	0.6	1.4	4.1	3.5
<i>Onychiurus similis</i>	2.9	3.8	1.2	2.5
<i>Onychiurus paro</i>	9.0	5.8	10.5	9.9
<i>Onychiurus affinis</i>	2.1	2.9	2.0	6.3
<i>Tullbergia granulata</i>	7.3	8.1	10.0	11.7
<i>Anurophorus binoculatus</i>	0.3	0.6	0.3	0.7
<i>Folsomia penicula</i>	63.1	42.3	40.1	26.5
<i>Metisotoma grandiceps</i>	0.1	0.5	0.3	0.7
<i>Micrisotoma achromata</i>	0.5	0.9	3.8	5.4
<i>Isotomiella minor</i>	48.0	58.5	79.6	104.7
<i>Isotoma notabilis</i>	4.6	5.0	4.2	3.5
<i>Isotoma trispinata</i>	4.1	4.0	7.0	4.7
<i>Isotoma manitobae</i>	1.5	3.7	0.5	1.6
<i>Isotoma viridis</i>	3.9	6.9	5.8	5.6
<i>Entomobrya multifasciata</i>	3.6	8.3	3.8	3.0
<i>Willowsia buski</i>	1.1	1.8	1.4	2.0
<i>Lepidocyrtus cyaneus</i>	0.0	0.0	1.1	1.9
<i>Tomoceris minor</i>	0.0	0.0	0.4	1.3
<i>Tomoceris sp</i>	0.1	0.1	0.3	0.7
<i>Sminthurinus quadrimaculatus</i>	0.4	1.0	0.7	1.0
<i>Dicytoma fusca</i>	0.0	0.0	0.2	0.6
Total mean density	167.9		185.9	
Total # species	23		28	

SPECIES	JUNE		JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	0.0	0.0	0.1	0.3	0.0	0.0
<i>Willemia denisi</i>	1.7	1.8	0.0	0.0	1.1	2.3
<i>Willemia intermedia</i>	0.8	1.6	1.1	1.7	4.2	4.4
<i>Friesea submilis</i>	2.5	2.5	3.6	5.8	8.8	12.8
<i>Pseudachorutes subcrassoides</i>	0.1	0.3	0.6	1.9	1.6	1.7
<i>Pseudachorutes aureofasciatus</i>	0.1	0.3	0.0	0.0	0.8	2.2
<i>Anurida pygmaea</i>	0.1	0.3	0.5	0.5	1.4	3.1
<i>Anurida furcifera</i>	0.7	1.3	0.2	0.3	0.0	0.0
<i>Neanura muscorum</i>	1.7	1.8	2.2	2.8	14.4	22.9
<i>Onychiurus similis</i>	5.0	5.3	3.4	3.7	0.7	0.9
<i>Onychiurus paro</i>	0.7	1.3	1.7	2.0	0.5	0.5
<i>Onychiurus affinis</i>	10.1	6.0	4.1	9.6	15.0	11.7
<i>Tullbergia granulata</i>	26.3	47.9	16.4	8.9	22.5	15.4
<i>Anurophorus binoculatus</i>	0.4	0.8	0.5	0.7	0.7	0.9
<i>Folsomia penicula</i>	38.1	30.8	45.7	43.8	146.4	168.8
<i>Metisotoma grandiceps</i>	0.0	0.0	0.1	0.3	0.1	0.3
<i>Micrisotoma achromata</i>	0.0	0.0	2.5	4.3	0.3	0.7
<i>Isotomiella minor</i>	24.7	12.0	20.7	13.3	21.3	2.3
<i>Isotomurus sp</i>	0.0	0.0	0.0	0.0	1.0	3.2
<i>Isotoma notabilis</i>	20.4	16.2	12.0	15.9	23.5	18.9
<i>Isotoma trispinata</i>	0.8	2.2	23.3	23.0	19.5	13.6
<i>Isotoma sp 3</i>	0.0	0.0	0.2	0.4	0.9	1.3
<i>Isotoma sp 5</i>	0.9	1.3	0.0	0.0	0.0	0.0
<i>Isotoma viridis</i>	0.2	0.4	0.2	0.4	0.1	0.3
<i>Entomobrya multifasciata</i>	0.0	0.0	12.1	29.1	3.7	3.7
<i>Orchesella cincta</i>	0.3	0.5	1.6	1.4	3.4	3.1
<i>Willowsia buski</i>	2.2	1.9	1.6	2.7	4.6	6.5
<i>Tomocerus minor</i>	0.0	0.0	0.0	0.0	0.1	0.3
<i>Neelus minimus</i>	0.3	0.5	0.7	0.8	7.0	10.3
<i>Sminthurinus quadrimaculatus</i>	0.0	0.0	0.1	0.3	0.0	0.0
<i>Sminthurinus henshawi</i>	0.8	0.9	0.0	0.0	0.0	0.0
<i>Dicyrtoma fusca</i>	0.1	0.3	0.0	0.0	0.3	0.1
Total mean density	139.0		155.2		303.9	
Total # species	24		25		27	

SPECIES	FD60-5		FD60-6	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	1.1	1.3	0.6	1.3
<i>Hypogastrura humi</i>	0.0	0.0	0.8	2.2
<i>Willemia denisi</i>	0.2	0.6	0.8	2.2
<i>Willemia intermedia</i>	4.5	4.7	6.4	7.5
<i>Friesea submilis</i>	2.6	2.0	10.5	10.1
<i>Friesea allaskella</i>	0.6	1.0	1.9	5.7
<i>Pseudachorutes subcrassoides</i>	0.3	0.5	0.6	0.7
<i>Pseudachorutes aureofasciatus</i>	0.0	0.0	0.1	0.3
<i>Anurida pygmaea</i>	1.9	1.9	0.7	1.0
<i>Anurida furcifera</i>	0.0	0.0	2.2	2.3
<i>Neamura muscorum</i>	5.1	3.8	4.2	4.7
<i>Onychiurus similis</i>	11.7	16.6	23.4	19.6
<i>Onychiurus paro</i>	5.7	6.3	6.1	7.8
<i>Onychiurus affinis</i>	31.7	12.8	3.0	5.1
<i>Tullbergia granulata</i>	35.7	30.9	25.7	25.3
<i>Anurophorus binoculatus</i>	1.6	1.6	1.3	2.4
<i>Folsomia penicula</i>	131.2	96.2	141.3	75.8
<i>Metisotoma grandiceps</i>	0.8	1.2	0.5	1.0
<i>Micrisotoma achromata</i>	0.9	0.9	3.9	6.4
<i>Isotomiella minor</i>	108.7	41.0	39.7	25.6
<i>Isotomurus sp</i>	0.3	1.0	0.0	0.0
<i>Isotoma notabilis</i>	4.0	4.7	56.0	54.5
<i>Isotoma trispinata</i>	36.0	23.8	2.6	4.0
<i>Isotoma sp 1</i>	1.1	1.2	1.4	1.9
<i>Isotoma sp 2</i>	0.0	0.0	1.2	1.4
<i>Isotoma viridis</i>	0.9	0.9	1.0	2.8
<i>Orchesella cincta</i>	0.3	0.7	0.4	1.0
<i>Entomobrya multifasciata</i>	0.0	0.0	0.3	0.5
<i>Willowsia buski</i>	0.0	0.0	2.0	3.5
<i>Nechus minimus</i>	7.1	8.2	12.4	17.2
<i>Arrhopalites benitus</i>	0.3	0.7	0.0	0.0
<i>Arrhopalites hirtus</i>	0.1	0.3	0.0	0.0
<i>Arrhopalites diversus</i>	0.1	0.3	0.2	0.4
<i>Sminthurinus quadrimaculatus</i>	0.0	0.0	0.3	0.5
<i>Sminthurus sp 2</i>	0.0	0.0	2.4	5.0
<i>Dicyrtoma fusca</i>	0.4	1.0	0.4	0.8
Total mean density	372.5		354.3	
Total # species	28		33	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	3.2	2.7	11.5	23.5
<i>Hypogastrura humi</i>	0.1	0.3	0.5	1.3
<i>Willemia denisi</i>	0.0	0.0	0.1	0.3
<i>Willemia intermedia</i>	0.9	1.4	1.0	1.7
<i>Friesea submillis</i>	0.5	1.2	0.0	0.0
<i>Friesea allinskella</i>	0.6	1.4	0.3	0.7
<i>Neanura muscorum</i>	0.3	0.7	0.1	0.7
<i>Pseudachorutes suberassoides</i>	1.4	2.5	1.0	1.3
<i>Anurida pygmaea</i>	0.5	0.7	0.8	1.0
<i>Anurida fureifera</i>	0.0	0.0	1.6	2.2
<i>Onychiurus similis</i>	11.8	9.1	4.1	3.4
<i>Onychiurus paro</i>	6.5	7.6	7.9	10.6
<i>Onychiurus affinis</i>	10.7	9.8	18.9	15.5
<i>Tullbergia granulata</i>	10.2	10.5	6.7	7.1
<i>Leurophorus binoculatus</i>	5.2	4.3	1.9	2.6
<i>Folsomia penicula</i>	179.8	122.8	226.1	166.3
<i>Metisotoma grandiceps</i>	2.0	3.0	3.7	7.2
<i>Microtoma achromata</i>	0.8	1.1	20.0	17.8
<i>Isotomiella minor</i>	125.7	67.8	46.5	31.3
<i>Isotomurus sp</i>	0.9	1.7	1.4	2.8
<i>Isotomurus palustroides</i>	0.0	0.0	0.7	1.6
<i>Isotoma notabilis</i>	4.7	6.5	24.0	30.1
<i>Isotoma trispinata</i>	8.8	11.0	18.5	18.5
<i>Isotoma manitobae</i>	1.3	1.0	1.0	3.2
<i>Isotoma hiemalis</i>	0.7	1.3	1.5	4.8
<i>Isotoma sp 1</i>	0.4	1.0	2.3	3.3
<i>Isotoma sp 2</i>	0.0	0.0	0.1	0.3
<i>Isotoma sp 3</i>	0.4	0.5	0.3	0.5
<i>Isotoma sp 4</i>	0.0	0.0	1.1	3.1
<i>Isotoma viridis</i>	0.7	1.3	0.7	1.3
<i>Orcheaella cineta</i>	0.7	2.2	0.0	0.0
<i>Eutomobrya multifasciata</i>	1.8	4.4	0.4	1.3
<i>Lepidocyrtus cyaneus</i>	0.0	0.0	0.3	0.5
<i>Tomocerus flavescens</i>	1.1	3.5	0.4	1.0
<i>Tomocerus sp</i>	4.1	3.0	2.4	6.9
<i>Neelus minimus</i>	0.0	0.0	0.5	0.8
<i>Smittthurides lepus</i>	0.1	0.3	15.3	14.4
<i>Arrhopalites benitus</i>	1.1	1.7	2.3	2.2
<i>Arrhopalites hirtus</i>	0.3	0.7	0.2	0.4
<i>Arrhopalites diversus</i>	0.7	1.6	0.8	1.3
<i>Smittthurinus quadrimaculatus</i>	0.2	0.4	0.1	0.3
<i>Smittthurinus sp 1</i>	1.2	1.5	0.3	0.7
<i>Smittthurinus sp 2</i>	0.2	0.4	0.1	0.3
<i>Dicyrtoma fusca</i>	0.0	0.0	0.6	1.1
unidentified	0.1	0.3	0.0	0.0
Total Mean density	389.8		428.9	
Total # species	38		43	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	1.9	4.7	3.5	3.8
<i>Hypogastrura lumi</i>	2.8	4.3	0.1	0.3
<i>Stenogasterura hiemalis</i>	0.0	0.0	0.1	0.3
<i>Willemia dentis</i>	0.7	1.6	0.7	2.8
<i>Willemia intermedia</i>	4.9	6.9	6.8	12.9
<i>Frieswa submissa</i>	1.4	1.4	1.2	1.4
<i>Frieswa alluscula</i>	0.7	0.8	2.6	4.2
<i>Pseudachorutes subcrassoides</i>	3.5	5.0	2.9	3.5
<i>Pseudachorutes aureofasciatus</i>	0.0	0.0	0.1	0.3
<i>Anurida pygmaea</i>	1.6	1.4	0.8	1.0
<i>Anurida forcifera</i>	2.8	4.2	3.4	9.4
<i>Neanura muscorum</i>	0.0	0.0	0.6	1.9
<i>Onychiurus similis</i>	9.6	6.6	10.6	20.5
<i>Onychiurus paro</i>	29.8	45.7	5.8	5.2
<i>Onychiurus affinis</i>	8.6	7.8	24.9	22.0
<i>Tullbergia granulata</i>	33.6	30.0	24.3	26.4
<i>Aurophorus binoculatus</i>	4.9	5.1	0.1	0.3
<i>Folsomia penicula</i>	164.8	151.0	269.4	223.0
<i>Micetozoma grandiceps</i>	6.8	9.9	15.8	27.3
<i>Micetozoma achromata</i>	10.5	9.9	19.5	19.6
<i>Isotomiella minor</i>	141.8	59.8	90.3	73.3
<i>Isotomurus sp</i>	5.9	7.0	3.8	6.6
<i>Isotomurus palustroides</i>	0.3	1.0	0.0	0.0
<i>Isotoma notabilis</i>	19.5	25.7	38.8	36.9
<i>Isotoma trispinata</i>	25.1	25.0	24.4	28.7
<i>Isotoma minutobae</i>	5.9	4.5	0.7	1.3
<i>Isotoma hiemalis</i>	0.2	0.4	0.1	0.3
<i>Isotoma sp 1</i>	2.0	5.7	1.2	2.5
<i>Isotoma sp 2</i>	0.1	0.3	0.0	0.0
<i>Isotoma sp 3</i>	0.8	1.5	0.2	0.6
<i>Isotoma sp 5</i>	0.0	0.0	2.7	3.6
<i>Isotoma viridis</i>	0.4	1.3	0.7	1.0
<i>Orchesella cincta</i>	0.4	1.3	0.1	0.3
<i>Entomobrya multifasciata</i>	6.7	6.8	1.3	2.8
<i>Smittthurinus quadrimaculatus</i>	0.3	0.7	0.0	0.0
<i>Tomocerus flavescens</i>	0.8	2.2	1.5	4.7
<i>Tomocerus sp</i>	7.0	5.8	2.6	2.8
<i>Neelus minimus</i>	14.3	12.3	2.4	2.4
<i>Neelus minimus</i>	0.0	0.0	0.2	0.6
<i>Neelus incertus</i>	0.0	0.0	0.1	0.3
<i>Smittthurides lepus</i>	1.9	3.0	0.2	0.6
<i>Arrhopalites benitus</i>	3.8	4.9	1.1	2.8
<i>Arrhopalites hirtus</i>	0.8	1.0	0.8	1.0
<i>Arrhopalites diversus</i>	2.1	2.6	0.2	0.6
<i>Smittthurinus henschawi</i>	0.0	0.0	0.1	0.3
<i>Smittthurinus sp 2</i>	1.1	3.1	0.0	0.0
<i>Dicyrtoma fusca</i>	0.1	0.3	0.0	0.0
unidentified	0.2	0.6	0.4	0.7
Total mean density	561.3		572.0	
Total # species	42		44	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	1.4	1.4	6.9	14.6
<i>Willemia dentis</i>	0.3	0.7	1.3	4.1
<i>Willemia intermedia</i>	10.1	11.7	3.2	5.1
<i>Friesea submitis</i>	1.1	1.7	1.1	1.6
<i>Friesea allaskella</i>	8.4	12.2	2.9	3.9
<i>Pseudachorutes subcrassoides</i>	0.1	0.3	0.3	0.7
<i>Pseudachorutes anreogfasciatus</i>	0.1	0.3	0.0	0.0
<i>Anurida pygmaea</i>	0.1	0.3	1.6	2.6
<i>Anurida forcifera</i>	2.2	4.6	0.7	1.2
<i>Neanura muscorum</i>	0.0	0.0	0.2	0.4
<i>Onychiurus similis</i>	6.4	3.9	3.6	6.6
<i>Onychiurus paro</i>	6.9	4.8	2.0	2.3
<i>Onychiurus affinis</i>	8.8	7.4	12.9	15.1
<i>Tullbergia granulata</i>	4.4	6.4	4.5	8.2
<i>Anurophorus binoculatus</i>	3.7	4.0	0.4	1.0
<i>Folsomia penicula</i>	52.0	50.7	37.5	61.7
<i>Metisotoma grandiceps</i>	2.6	4.1	2.4	3.8
<i>Micrisotoma achromata</i>	8.0	7.5	9.3	7.2
<i>Isotomiella minor</i>	50.3	20.1	29.5	20.1
<i>Isotomurus sp</i>	0.2	0.4	8.5	14.1
<i>Isotoma notabilis</i>	7.9	8.6	16.0	14.5
<i>Isotoma trispinata</i>	22.9	17.5	20.4	19.6
<i>Isotoma multitubae</i>	20.6	29.9	1.3	4.1
<i>Isotoma hiemalis</i>	0.7	2.2	1.2	3.4
<i>Isotoma sp 1</i>	0.3	0.5	2.3	4.0
<i>Isotoma sp 2</i>	0.1	0.3	1.7	5.4
<i>Isotoma sp 3</i>	0.5	0.7	0.1	0.3
<i>Isotoma sp 4</i>	0.0	0.0	0.3	0.7
<i>Isotoma sp 5</i>	0.0	0.0	1.4	3.8
<i>Isotoma viridis</i>	0.3	0.7	0.1	0.3
<i>Orchesella cincta</i>	2.6	5.7	3.5	7.3
<i>Entomobrya multifasciata</i>	7.2	12.1	0.1	0.3
<i>Lepidocyrtus cyaneus</i>	0.0	0.0	0.2	0.4
<i>Tomocerus minor</i>	0.0	0.0	0.1	0.3
<i>Tomocerus sp</i>	1.1	1.1	6.8	9.7
<i>Neelus minimus</i>	6.7	11.9	25.1	35.7
<i>Neelus minutus</i>	0.0	0.0	3.2	5.1
<i>Neelus incertus</i>	0.3	0.7	4.5	6.6
<i>Sminthurides lepus</i>	1.0	2.2	2.7	2.9
<i>Arrhopalites benitus</i>	2.1	3.1	4.2	6.4
<i>Arrhopalites hirtus</i>	0.0	0.0	0.2	0.4
<i>Arrhopalites diversus</i>	0.6	0.8	0.0	0.0
<i>Sminthurus sp 2</i>	1.6	3.9	0.4	1.4
<i>Dicyrtoma fusca</i>	0.0	0.0	0.2	0.4
unidentified	0.0	0.0	0.5	0.7
Total mean density	243.5		211.6	
Total # species	37		43	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricula</i>	0.5	0.9	3.0	3.3
<i>Hypogastrura humi</i>	0.0	0.0	0.1	0.3
<i>Willmannia denisi</i>	2.1	5.0	0.7	1.2
<i>Willmannia intermedia</i>	3.8	5.6	4.1	11.6
<i>Friesen submilis</i>	1.1	2.0	0.4	0.5
<i>Friesen alaskella</i>	7.9	16.7	1.5	2.8
<i>Pseudochorutes subcrassoides</i>	1.2	1.8	0.7	1.1
<i>Pseudochorutes aureofasciatus</i>	1.4	4.4	0.0	0.0
<i>Anurida pygmaea</i>	3.9	5.6	2.3	2.8
<i>Anurida furcifera</i>	9.2	13.6	2.4	5.6
<i>Neanura muscorum</i>	0.1	0.3	0.9	1.9
<i>Orychiurus similis</i>	5.9	7.2	2.2	2.5
<i>Orychiurus puro</i>	7.8	5.4	4.4	4.9
<i>Orychiurus affinis</i>	7.2	8.7	10.7	13.0
<i>Tullbergia granulata</i>	19.7	22.2	6.8	8.0
<i>Amorophorus binoculatus</i>	0.8	1.5	0.4	1.3
<i>Folsomia penicula</i>	77.3	51.6	137.9	163.7
<i>Metisotoma grandiceps</i>	4.6	5.9	4.5	6.2
<i>Aficristotoma ochromata</i>	4.0	5.2	6.8	4.9
<i>Isotomiella minor</i>	116.6	84.0	30.4	20.8
<i>Isotomurus</i> sp	7.4	19.0	0.6	1.0
<i>Isotoma ekmani</i>	0.0	0.0	1.6	5.1
<i>Isotoma notabilis</i>	9.4	15.1	26.8	16.4
<i>Isotoma trispinatus</i>	21.3	32.7	15.5	10.0
<i>Isotoma minutus</i>	12.3	23.6	0.2	0.6
<i>Isotoma hiemalis</i>	0.1	0.3	0.1	0.3
<i>Isotoma</i> sp 1	0.1	0.3	0.1	0.3
<i>Isotoma</i> sp 2	0.1	0.3	0.0	0.0
<i>Isotoma</i> sp 3	0.2	0.6	0.0	0.0
<i>Isotoma</i> sp 4	0.0	0.0	3.5	7.3
<i>Isotoma</i> sp 5	0.0	0.0	3.0	6.0
<i>Isotoma viridis</i>	0.4	1.0	0.4	1.3
<i>Orchesella cincta</i>	0.0	0.0	4.3	4.5
<i>Entomobrya multifasciata</i>	7.4	8.9	2.0	3.0
<i>Tomocerius minor</i>	0.4	1.0	0.4	0.7
<i>Tomocerius</i> sp	2.3	2.7	2.7	3.2
<i>Necurus minutus</i>	4.5	4.6	8.8	17.7
<i>Necurus minutus</i>	0.0	0.0	0.1	0.3
<i>Necurus incertus</i>	0.3	1.0	0.8	1.9
<i>Smindulus lepus</i>	3.7	6.0	2.2	3.3
<i>Arrhopalites beutius</i>	5.1	5.9	2.4	2.4
<i>Arrhopalites hirtus</i>	1.5	2.7	0.6	2.0
<i>Arrhopalites diversus</i>	2.4	3.1	0.0	0.0
<i>Smindulus quadrimaculatus</i>	0.2	0.4	0.0	0.0
<i>Smindulus</i> sp 1	2.5	4.3	0.3	0.5
<i>Smindulus</i> sp 2	0.2	0.4	0.0	0.0
<i>Dicyrtoma fusca</i>	0.0	0.0	0.3	0.7
unidentified	0.0	0.0	0.5	0.7
Total mean density	357.1		297.2	
Total # species	40		41	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	0.2	0.4	0.4	0.5
<i>Willemia intermedia</i>	1.1	1.7	0.3	0.7
<i>Friesea submillis</i>	0.4	1.0	0.1	0.3
<i>Friesea alaskella</i>	1.1	1.7	0.3	0.7
<i>Pseudachorutes subcrassoides</i>	0.0	0.0	0.5	1.0
<i>Anurida pygmaea</i>	1.0	1.0	1.2	2.2
<i>Anurida fureifera</i>	5.1	13.7	0.1	0.3
<i>Neanura muscorum</i>	0.3	0.5	1.9	3.7
<i>Onychiurus similis</i>	4.5	2.8	1.3	2.4
<i>Onychiurus pavo</i>	7.5	12.1	3.6	3.8
<i>Onychiurus affinis</i>	20.8	17.9	19.4	21.9
<i>Tullbergia granulata</i>	4.2	3.2	2.1	2.6
<i>Anurophorus binoculatus</i>	2.8	2.1	2.7	7.0
<i>Folsomia penicula</i>	112.1	121.5	60.5	46.4
<i>Metisotoma grandiceps</i>	6.0	4.1	5.1	5.7
<i>Micrisotoma achromata</i>	2.8	2.1	2.7	7.0
<i>Isotomiella minor</i>	82.2	54.2	59.1	47.9
<i>Isotomurus sp</i>	16.9	26.4	26.5	34.5
<i>Isotomurus palustris</i>	0.0	0.0	10.3	18.7
<i>Isotoma notabilis</i>	17.2	20.8	35.2	27.0
<i>Isotoma trispinata</i>	23.7	26.1	23.1	25.0
<i>Isotoma manitobae</i>	0.1	0.3	0.0	0.0
<i>Isotoma viridis</i>	0.4	0.7	0.8	1.9
<i>Orchesella cincta</i>	3.8	4.6	7.2	9.9
<i>Entomobrya multifasciata</i>	0.4	0.7	2.3	3.0
<i>Tomocerus minor</i>	0.2	0.4	0.4	0.8
<i>Tomocerus sp</i>	0.0	0.0	2.1	3.5
<i>Neelus minimus</i>	53.7	53.7	26.2	20.2
<i>Neelus minutus</i>	0.0	0.0	1.2	1.6
<i>Neelus incertus</i>	0.6	2.0	2.3	3.7
<i>Sminthurides lepus</i>	0.0	0.0	0.4	0.7
<i>Arrhopalites benitus</i>	0.1	0.3	0.1	0.3
<i>Arrhopalites diversus</i>	0.3	0.5	0.0	0.0
<i>Sminthurinus quadrimaculatus</i>	0.0	0.0	0.5	1.3
<i>Sminthurus sp 2</i>	0.0	0.0	0.3	0.7
Total mean density	380.6		549.0	
Total # species	29		35	

SPECIES	JULY		AUGUST	
	MEAN	STD. DEV	MEAN	STD. DEV
<i>Hypogastrura loricata</i>	0.3	0.5	0.9	2.8
<i>Hypogastrura humi</i>	0.2	0.6	0.0	0.0
<i>Willemia densa</i>	0.4	0.7	0.0	0.0
<i>Willemia intermedia</i>	1.0	1.4	0.0	0.0
<i>Friesea subnilis</i>	0.8	1.2	4.1	7.6
<i>Friesea alaskella</i>	0.7	2.2	1.7	4.0
<i>Pseudachorutes suberassoides</i>	1.2	2.1	0.1	0.3
<i>Pseudachorutes aureofasciatus</i>	0.2	0.6	0.0	0.0
<i>Anurida pygmaea</i>	3.5	4.9	0.4	1.3
<i>Anurida furcifera</i>	1.5	1.8	1.9	4.3
<i>Neanura muscorum</i>	0.7	1.1	0.3	1.0
<i>Onychiurus similis</i>	7.3	8.7	2.9	5.5
<i>Onychiurus paro</i>	13.7	8.3	0.6	1.0
<i>Onychiurus affinis</i>	18.8	11.2	1.7	2.6
<i>Tullbergia granulata</i>	23.6	19.9	2.8	6.5
<i>Anurophorus bioculatus</i>	4.2	4.5	0.0	0.0
<i>Pisidium penicula</i>	166.1	177.1	12.0	24.8
<i>Actisotoma grandiceps</i>	7.0	5.1	0.2	0.4
<i>Actisotoma achromata</i>	10.2	7.3	0.5	1.0
<i>Isotomiella minor</i>	85.1	53.2	23.0	32.2
<i>Isotomurus</i> sp	0.3	0.5	83.7	35.0
<i>Isotomurus palustrisoides</i>	0.0	0.0	23.8	18.8
<i>Isotoma notabilis</i>	7.4	5.8	5.7	11.8
<i>Isotoma trispinata</i>	37.7	44.4	6.7	14.5
<i>Isotoma manitobae</i>	0.8	2.5	0.0	0.0
<i>Isotoma</i> sp 1	1.2	1.6	1.4	2.7
<i>Isotoma</i> sp 3	0.1	0.3	0.0	0.0
<i>Isotoma</i> sp 4	0.0	0.0	8.0	23.5
<i>Isotoma</i> sp 5	0.1	0.3	0.0	0.0
<i>Isotoma viridis</i>	0.6	1.1	0.0	0.0
<i>Orchesella cincta</i>	0.1	0.3	1.4	2.6
<i>Entomobrya multifasciata</i>	4.3	6.7	0.3	0.7
<i>Willmannia buski</i>	0.1	0.3	1.4	2.6
<i>Tomocerus minor</i>	0.0	0.0	8.0	23.5
<i>Tomocerus</i> sp	0.3	1.0	0.1	0.3
<i>Neelus minimus</i>	41.0	72.6	5.0	6.5
<i>Neelus minutus</i>	0.1	0.3	0.4	0.5
<i>Neelus incertus</i>	0.2	0.4	6.4	9.2
<i>Sminthurides lepus</i>	0.1	0.3	0.1	0.3
<i>Arrhopalites benitus</i>	0.2	0.4	0.3	1.0
<i>Arrhopalites diversus</i>	0.9	2.5	0.2	0.6
<i>Sminthurinus quadrimaculatus</i>	1.8	2.0	0.4	1.3
<i>Sminthurinus henshawi</i>	0.2	0.4	0.3	0.5
<i>Sminthurus</i> sp 1	0.4	0.7	0.1	0.3
<i>Sminthurus</i> sp 2	0.5	0.8	1.4	3.8
<i>Dicyrtoma fusca</i>	0.1	0.3	0.1	0.3
Total mean density	445.3		209.4	
Total # species	43		38	

Appendix B. Shannon-Weiner diversity indices for Collembola in the upper and lower halves of the soil samples collected from 3 different aged FD forest, summers 1992 to 1994.

Area, Date, Site	Layers	# Specimens (# species)	Shannon-Weiner index	
			H'	Evenness
FDO, JULY '92				
FDO-1	Upper	5243 (34)	3.5	0.68
	Lower	2260 (27)	2.9	0.60
FDO-2	Upper	4163 (34)	3.1	0.61
	Lower	2000 (27)	2.6	0.56
AUG. '92				
FDO-1	Upper	2140 (31)	2.8	0.60
	Lower	1237 (30)	3.0	0.61
FDO-2	Upper	2687 (28)	2.4	0.49
	Lower	1185 (27)	2.7	0.56
JUNE '93				
FDO-1	Upper	5107 (39)	2.2	0.41
	Lower	1871 (29)	2.1	0.43
FDO-2	Upper	6417 (36)	2.1	0.41
	Lower	2519 (29)	2.3	0.48
JULY '93				
FDO-1	Upper	5250 (33)	1.6	0.32
	Lower	1811 (28)	2.2	0.45
FDO-2	Upper	3737 (31)	2.5	0.51
	Lower	1703 (26)	2.0	0.43
AUG. '93				
FDO-1	Upper	3725 (30)	2.2	0.45
	Lower	2462 (28)	1.9	0.40
FDO-2	Upper	5218 (33)	2.1	0.42
	Lower	1586 (30)	2.1	0.42
JUNE '94				
FDO-1	Upper	6728 (41)	3.1	0.57
	Lower	1772 (30)	2.5	0.52
FDO-2	Upper	6234 (42)	2.3	0.44
	Lower	2242 (32)	2.2	0.45
FD40, JULY '92				
FD40-3	Upper	3296 (21)	2.2	0.51
	Lower	502 (19)	2.5	0.59
FD40-4	Upper	3283 (21)	2.6	0.60
	Lower	1709 (21)	2.5	0.58
AUG. '92				
FD40-3	Upper	2773 (22)	2.1	0.47
	Lower	760 (20)	2.9	0.66
FD40-4	Upper	2344 (21)	2.5	0.56
	Lower	819 (20)	2.5	0.58
JUNE '93				
FD40-3	Upper	3351 (24)	2.0	0.44
	Lower	2076 (22)	2.4	0.54
FD40-4	Upper	5258 (23)	1.8	0.40
	Lower	1840 (18)	1.8	0.43

Appendix B Cont.....

Area Date, site	Layers	# Specimens (# Species)	Shannon-Weiner index	
			H'	EEvenness
JULY '93				
FD40-3	Upper	2392 (28)	2.6	0.55
	Lower	1302 (20)	2.3	0.53
FD40-4	Upper	3636 (28)	2.1	0.44
	Lower	2059 (19)	1.6	0.39
AUG. '93				
FD40-3	Upper	1985 (25)	2.7	0.57
	Lower	2357 (24)	2.5	0.54
FD40-4	Upper	2824 (27)	2.2	0.47
	Lower	3100 (21)	2.0	0.45
JUNE '94				
FD40-3	Upper	3341 (23)	2.6	0.57
	Lower	1356 (23)	2.5	0.55
FD40-4	Upper	5414 (26)	2.5	0.54
	Lower	2031 (23)	2.0	0.45
FD60, JULY '92				
FD60-5	Upper	2956 (22)	2.3	0.51
	Lower	1056 (22)	2.6	0.58
FD60-6	Upper	2386 (24)	2.8	0.61
	Lower	967 (20)	2.3	0.54
AUG. '92				
FD60-5	Upper	1045 (25)	3.0	0.64
	Lower	385 (22)	3.2	0.72
FD60-6	Upper	1503 (25)	2.6	0.57
	Lower	346 (23)	3.2	0.71
JUNE '93				
FD60-5	Upper	1829 (24)	2.4	0.52
	Lower	1055 (22)	2.3	0.52
FD60-6	Upper	945 (23)	2.9	0.63
	Lower	445 (18)	2.3	0.55
JULY '93				
FD60-5	Upper	2117 (24)	2.8	0.61
	Lower	784 (21)	2.6	0.60
FD60-6	Upper	1255 (23)	3.1	0.68
	Lower	297 (18)	3.0	0.54
AUG. '93				
FD60-5	Upper	1885 (28)	3.1	0.63
	Lower	1090 (24)	2.2	0.49
FD60-6	Upper	1969 (26)	3.1	0.66
	Lower	1070 (19)	2.3	0.53
JUNE '94				
FD60-5	Upper	2605 (25)	2.8	0.60
	Lower	844 (24)	2.5	0.55
FD60-6	Upper	2723 (31)	2.9	0.59
	Lower	820 (30)	3.2	0.64

Appendix C. Two Way Indicator Species Analysis table showing the classification of forests with indicator species of Collembola.



